ONTOGENETIC CHANGES IN LIMB BONE STRUCTURAL PROPERTIES AND LOCOMOTOR BEHAVIOR IN *PAN*

by
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ABSTRACT

As our closest living relatives, chimpanzees have often served as models to help reconstruct early hominin behavior. However, despite documented behavioral variation at the species and subspecies level, we still know little about how skeletal variation relates to behavior among living chimpanzees. This is especially important in light of increasing evidence that early hominins engaged in a variety of locomotor modes involving mixtures of arboreal and terrestrial behaviors: previous studies have often focused on broad taxonomic and behavioral groups, but closely-related modern taxa with subtle behavioral differences may provide better models. Studies of ontogenetic trajectories within groups can also serve as "natural experiments" for testing the relationship of morphology to known behavioral changes with age while controlling for genetic heritage.

This study compares skeletal morphology with field observational behavioral data among bonobos and the individual subspecies of common chimpanzee. Aspects of skeletal morphology previously hypothesized to reflect locomotor behavior, including bone lengths, articular proportions, phalangeal curvature and dorsal metacarpal and metatarsal ridge (DMR) morphology, and cross-sectional structural properties (e.g. inter-limb strength proportions, diaphyseal shape ratios), were compared both across adult *P. paniscus* and *P. troglodytes* subspecies and during ontogeny. These results were then contextualized in existing data on locomotor behavior frequencies in these same taxa. Bone lengths and articular proportions were hypothesized to primarily reflect genetic differences and thus mainly vary along phylogenetic lines, while internal cross-sectional geometry, phalangeal curvature, and the DMR were predicted to show greater concordance with behavior regardless of phylogenetic relationships.

Results suggest that, even at these narrow taxonomic levels, length and articular proportions primarily vary along taxonomic lines, distinguishing *P. paniscus* from other *Pan,* while cross-sectional geometry and phalangeal curvature show more differences between *P. troglodytes* subspecies and are more consistent with differences in frequencies of locomotor behavior. Dorsal metacarpal ridge morphology seemed to be related both to body size and to behavior. This increased understanding of the relative importance of genetic inheritance and developmental plasticity in the production of adult skeletal features in *Pan* informs both our understanding of the functional anatomy of living hominoids and our interpretations of morphological variation in fossil hominins.

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1 INTRODUCTION AND RESEARCH DESIGN

1.1 RATIONALE

Although postcranial morphology is often used to infer locomotor behavior in fossils through comparison with extant taxa (e.g. McHenry and Berger, 1998; Harcourt-Smith and Aiello, 2004; Ruff, 2008a; Lovejoy et al., 2009; Pontzer et al., 2010; Ward et al., 2011; Zipfel et al., 2011; Haile-Selassie et al., 2012), this process is complicated by the fact that fossil taxa often exhibit "mosaic" combinations of traits, or are intermediate in morphology between different modern taxa. Living animals are therefore not always useful as direct functional analogs. This is becoming increasingly evident for both the fossil hominin and Miocene ape lineages. For example, *Australopithecus sediba* combined both human and ape-like hand and foot morphology with a more human-like pelvis (Berger et al., 2010; Kivell et al., 2011; Zipfel et al., 2011), and both the hand and foot of recently described *Homo naledi* show mosaics of features thought to reflect more modern human-like manipulative and locomotor behavior, along with retention of climbing capabilities (Harcourt-Smith et al., 2015; Kivell et al., 2015). Many Miocene apes similarly display mixtures of "ape-like" and "monkey-like" morphology (Almécija et al., 2009; Begun and Kivell, 2011; Alba et al., 2012).

Because early hominins are clearly a radiation of closely-related forms that diversified rapidly and seem to exhibit a variety of subtly different locomotor adaptations (Fleagle, 2013), an understanding of the extent to which morphology is reflective of small differences in the frequencies of different behaviors in closely related taxa is key to reconstructing their biology (Ward, 2013). Despite this, many past studies of these issues have involved broad comparisons of morphological differences between taxa that are

disparate both genetically and behaviorally (e.g., chimpanzees or African apes vs. modern humans). Given the increasingly complex picture of fossil locomotor diversity, this method is ultimately of limited utility, as modern humans are separated by millions of years of evolution from their last common ancestor with chimpanzees (the morphology of which is not known), and differ drastically in locomotor behavior from all other living apes (Sarich and Wilson, 1967; Richmond et al., 2001; Langergraber et al., 2012). Instead, in order to use studies of morphological variation in extant taxa to address fossil hominin variation, it may be more productive to carry out more controlled comparisons between closely-related species or subspecies that vary along gradients of behavior — relative frequencies of climbing, suspension, leaping, arboreal and terrestrial quadrupedalism — rather than simply employing an arboreal—terrestrial dichotomy. These types of narrow comparisons necessitate detailed quantitative morphological and behavioral data at the subspecies level, but are especially necessary because not all "arboreal" or "terrestrial" behaviors impact the skeleton in the same way: for example, pure suspension may not generate as much bending strain in the forelimb as other types of forelimb-dominated arboreal behaviors such as climbing (Swartz et al., 1989), and even within a single behavioral category such as arboreal quadrupedalism, kinematics may change depending on the type of arboreal substrate used (Schmitt, 2003). Fine-grained studies of closely-related taxa are better able to take into account these types of differing mechanical environments. Combining these approaches with ontogenetic analyses within taxa, which can also shed light on behavior-morphology relationships on a finer scale (Ruff et al., 2013; Burgess et al., 2016; Sarringhaus and MacLatchy, 2016; Young and Booth, 2016), can ultimately provide a more complete understanding of the

relationships between morphology and behavior and thereby provide a better basis for locomotor reconstruction in fossils.

This dissertation uses the genus *Pan* as a model to explore these issues. Biomechanically relevant aspects of postcranial skeletal morphology that have been linked with locomotor behavior across broad groups of primates are examined in this narrow taxonomic framework. Analyses incorporate comparisons of adults and examination of ontogenetic variation both between and within species and subspecies, with results specifically contextualized in existing behavioral literature.

1.2 ORGANIZATION OF DISSERTATION

This chapter provides the theoretical framework and background for the dissertation. It includes both a discussion of genetic, morphological, and ecological variation in *Pan* and a summary of previous studies establishing differential plasticity of aspects of skeletal morphology, focusing on studies of primates and great apes. Chapter 2, Materials and Methods, presents an overview of the sample used in the current study and discusses the methodology for collection of skeletal morphological data, estimation of chronological age, and selection and collation of literature behavioral data. Statistical procedures used for data analysis are also reviewed. The results of these analyses are presented in Chapter 3 and Chapter 4, organized by skeletal variable and region according to the research questions of the dissertation (see below). Chapter 5 summarizes and contextualizes the results of the dissertation. All supplementary data are included in the Appendix.

1.3 CONCEPTUAL FRAMEWORK

1.3.1 Genetic and ecological variation in *Pan*

The genus *Pan* is a natural group for this type of study, because it incorporates a number of different taxonomic subdivisions as well as substantial behavioral and ecological variability amongst its members. It includes two species, *P. paniscus* (bonobos or pygmy chimpanzees) and *P. troglodytes* (common chimpanzees). On the basis of both morphological and genetic evidence, the latter has been conventionally divided into three geographically distinct subspecies (Figure 1.1): *P. t. schweinfurthii* in eastern Africa, *P. t. troglodytes* in central Africa, and *P. t. verus* in western Africa (Gordon et al., 2013), although morphology has not always unequivocally supported these (Shea and Coolidge, 1988; Groves et al., 1992). Bonobos have been found to be genetically distinct from all common chimpanzees, and studies generally show that *P. t. verus* are more distantly related to *P. t. troglodytes* and *P. t. schweinfurthii* than either of these two is to each other (Won and Hey, 2004; Gonder et al., 2006; Caswell et al., 2008; Hey, 2010; Wegmann and Excoffier, 2010; Bjork et al., 2011; Gonder et al., 2011; Langergraber et al., 2012; Prado-Martinez et al., 2013). However, there has been disagreement over whether the latter two subspecies should rather be represented as a single taxon, as they have not been consistently resolved as monophyletic groups (Fischer et al., 2006; Gonder et al., 2011; Fünfstück et al., 2015). This is likely because they are characterized by a degree of clinal genetic variation such that individuals who are geographically closer to one another are also genetically closer, so the spatial distribution of individuals used in the study likely affects the results (Fünfstück et al., 2015). Recent studies using more complete, high-coverage genetic data also have found evidence of a more complex population history for

bonobos and common chimpanzees than previously recognized, with some possible instances of ancient admixture between bonobos and central common chimpanzees (or their ancestors) over the past 1-3 thousand years (de Manuel et al., 2016).

More recently, a fourth subspecies, *P. t. ellioti* (originally *vellerosus*) has been erected based on genetic evidence (Gonder et al., 2006; 2011). This population is genetically closest to *P. t. verus*, but is geographically closer to the current distribution of *P. t. troglodytes*, separated from them by the Sanaga River in Cameroon (Bjork et al., 2011; Gonder et al., 2011). (For a more detailed review of these topics, see Pilbrow et al. (2006)).

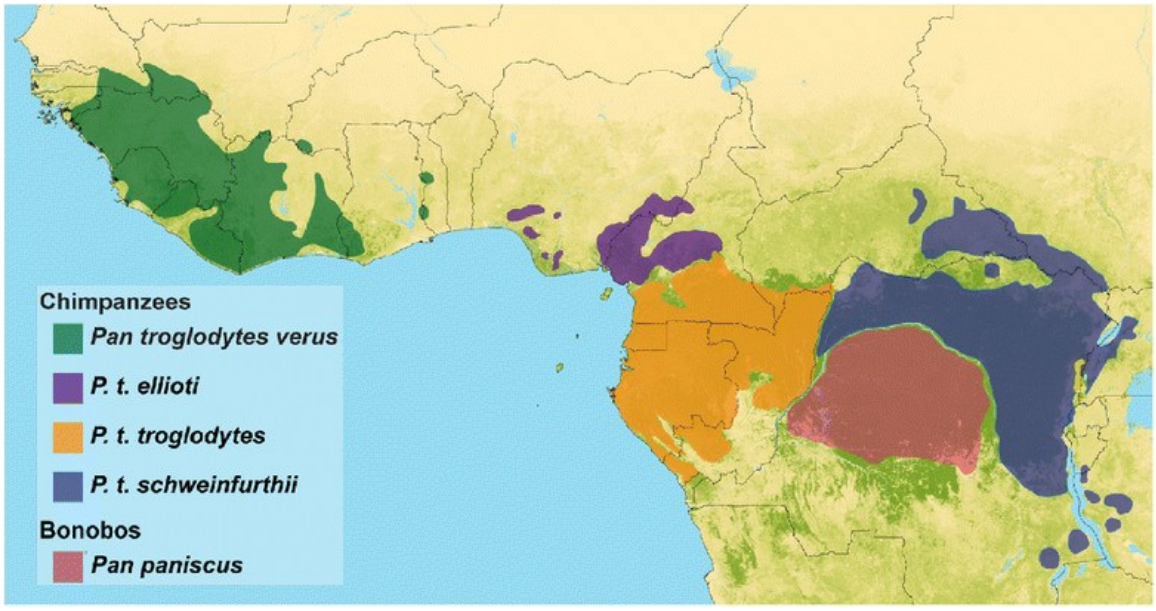

Figure 1.1 Current geographic distribution of the genus Pan. *Figure from Clee et al., 2015.*

Most studies place the split between bonobos and common chimpanzees at around 1 million year ago, although some estimates are as high as 1.8 million or as low as 750 thousand years (Won and Hey, 2004; Caswell et al., 2008; Hey, 2010; Wegmann and Excoffier, 2010; Gonder et al., 2011; Langergraber et al., 2012; Prado-Martinez et al.,

2013). *P. t. verus* split from the remaining two subspecies around 400-500 thousand years ago (Caswell et al., 2008; Hey, 2010; Wegmann and Excoffier, 2010; Bjork et al., 2011; Gonder et al., 2011; Prado-Martinez et al., 2013). When they are found to be genetically distinct, most studies suggest that *P. t. troglodytes* and *P. t. schweinfurthii* diverged around 200 thousand years ago, although estimates for this date range up to 500 thousand years (Caswell et al., 2008; Hey, 2010; Wegmann and Excoffier, 2010; Bjork et al., 2011; Prado-Martinez et al., 2013).

Some of this variation in results may be due to methodological differences between studies, as different types of DNA are sensitive to changes over different time periods: nuclear genes on the order of millions of years, haploid genes like mtDNA over tens or hundreds of thousands of years, and micro satellite loci over even more recent time spans (Gagneux et al., 2001). Additionally, studies of mtDNA and y chromosome DNA will be affected by sex dispersal patterns (Langergraber et al., 2014). Studies using generation times rather than genetic data have produced the oldest estimates for divergence dates (Langergraber et al., 2012). Despite these differences, it is clear that all members of the genus *Pan* are closely related to one another, having diverged within the Pleistocene, and occupy geographically distinct regions today.

In accordance with these geographic differences, environmental variables, including seasonality, elevation, openness of terrain, and habitat structure also vary among different species and subspecies of *Pan* (Table 1.1). Habitat conditions across the bonobo range are relatively uniform: primary evergreen forests with some swampy areas, at a fairly constant altitude and rainfall level, without a true dry season (White, 1986; Reinartz et al., 2000; Waller, 2011). Annual rainfall at one site was reported at 1960mm,

with temperature ranging from 20 to 29°C (Doran, 1989). Habitat is less consistent in common chimpanzees, both between and sometimes within subspecies. *P. t. verus*, the western-most subspecies, inhabits a range of habitats (Waller, 2011), but the Taï Forest, where this subspecies has been studied most thoroughly, has an average annual rainfall of 1800mm, average annual temperature of 24°C, and two rainy seasons (Boesch and Boesch, 1983; Doran, 1989). *P. t. troglodytes* also lives in tropical rainforest, with one site reporting two rainy seasons and a similar average annual rainfall, from 1400-1700mm (Kuroda et al., 1996).

Table 1.1 Characteristics of P. troglodytes *study sites**

Site	**Country**	**Taxon**	**Description**	**Mean Annual Rainfall (mm)**	**Elevation (m)**
Taï Forest	Ivory Coast	*P. t. verus*	Tropical rainforest	1829	202
Bossou	Guinea	*P. t. verus*	Tropical forest	2230	550
Mt. Assirik	Senegal	*P. t. schw.*	Savannah woodland	954	100-311
Gombe	Tanzania	*P. t. schw.*	Riverine forest/woodland	1775	1137
Mahale	Tanzania	*P. t. schw.*	Riverine forest/woodland	1836	1040
Kibale (Kanyawara)	Uganda	*P. t. schw.*	Moist evergreen forest	1671	1500
Kibale (Ngogo)	Uganda	*P. t. schw.*	Moist evergreen forest	1800	1400
Budongo	Uganda	*P. t. schw.*	Moist tropical rainforest	1842	1100

* *Modified from Stumpf* (2007) *and Waller* (2011). *Not all sites have corresponding locomotor behavioral data (see* Table 1.3*)*

P. t. schweinfurthii is found in a wide variety of habitats (Table 1.1). They have most commonly been studied at sites such as Mahale and Gombe in Tanzania, which are described as riverine forests (although Gombe is somewhat more variable than Mahale,

see below), and at Kanyawara, Ngogo, and Budongo in Uganda, which are evergreen or tropical rainforests. These sites generally have a single rainy season, but vary in mean annual rainfall, elevation, and openness of terrain (Collins and McGrew, 1988). However, *P. t. schweinfurthii* are also found in low-elevation, arid environments such as Assirik and Semliki, which have much lower annual rainfall (Hunt and McGrew, 2002), and there are even differences in openness of ground cover between Mahale and Gombe, which are more similar in other respects (Hunt, 1989). Habitat therefore differs both between and among the closely related species and subspecies of *Pan*, but does not completely track genetic differences as bonobo habitats resemble those of some common chimpanzee subspecies (*P. t. schweinfurthii*) more than others and there is more habitat variation within one subspecies than occurs within the others (also see Clee et al., 2015).

1.3.2 Morphological variation in *Pan*

A number of studies have documented postcranial morphological variation between species and subspecies of *Pan*. Those most relevant to the current work are discussed in this section and summarized in Table 1.2. In general, there are relatively few systematic proportional differences between common chimpanzee subspecies, but they do differ in both overall size and absolute body measurements both between and within subspecies. In body mass, *P. t. schweinfurthii* as a whole are smaller than *P. t. troglodytes*, with average male and female body masses of 43.0 and 33.2 kg in the former and 60 and 47.4 kg in the latter (as recorded in museum records and field studies, Jungers and Susman (1984)).There is also a degree of body mass variation within *P. t. schlikekuweinfurthii*: in particular, the Gombe population is smaller than others, with an average body mass of 39.0 kg in males and 31.3 kg in females (Pusey et al., 2005).

Individuals from other populations tend to be several kilograms heavier on average, with male averages ranging from 42.0-43.0 kg and females from 34.3-36.9kg (Carter et al., 2008). *P. t. troglodytes* may also have regional variation in body mass, but are less well studied. There are very few available body masses for *P. t. verus*, but it has been suggested that they are slightly larger than *P. t. schweinfurthii,* although more similar in size to *P. t. schweinfurthii* than to *P. t. troglodytes* (a single male *P. t. verus* specimen has a recorded body mass of 46.4 kg, Jungers and Susman (1984)). In keeping with their smaller overall size, Gombe *P. t. schweinfurthii* also have absolutely shorter limbs than both other regional populations of their subspecies and Taï Forest *P. t. verus* (Zihlman et al., 2008), although the Mahale population of *P. t. schweinfurthii* may also be similar to Gombe in absolute limb length (Carlson et al., 2010). They also have smaller acetabulae than at least *P. t. verus* (Zihlman et al., 2008).

There are clearer distinctions in general morphology between species in *Pan*, with bonobos differing in a number of ways from common chimpanzees. In his first extensive morphological description of the taxon, Coolidge (1933) discussed the rounder neurocrania and less prognathic faces of bonobos compared to those of common chimpanzees. Coolidge also argued that bonobos are "dwarfed" relative to chimpanzees. However, further examination revealed that bonobos are actually similar in body mass to *P. t. schweinfurthii* (males average 45.0kg and females 33.2 kg, Jungers and Susman (1984)), but smaller than other subspecies. Thus, morphological differences between *P. paniscus* and *P. t. schweinfurthii* cannot be explained by allometric scaling (Jungers and Susman, 1984). Bonobos are generally described as more "gracile" in body proportions than all *P. troglodytes* (Zihlman and Cramer, 1978). Overall gracility and smaller body

mass than (at least some) common chimpanzees has been linked by some researchers to active arboreal behavior (Susman et al., 1984). This appearance of gracility is partly due to proportional differences in the shoulder and pelvic girdle, where bonobos have shorter clavicles and relatively narrower scapulae than common chimpanzees (Zihlman and Cramer, 1978; Shea, 1986). These scapular differences have been interpreted as morphological paedomorphism in *P. paniscus* possibly, although not necessarily, related to more active, acrobatic locomotor behavior (Shea, 1986; Doran, 1993). As bonobos and common chimpanzees are actually similar in chest girth relative to trunk length (Coolidge and Shea, 1982), bonobos' overall appearance of gracility is likely also driven by the length of their limbs, especially the hindlimb. Despite the differences in body weight discussed above, average absolute hindlimb length is similar (within sexes) in all *Pan* species and subspecies. Thus, bonobos have relatively longer hind limbs relative to both their body mass and trunk height (Shea, 1981; Morbeck and Zihlman, 1989). In contrast, differences in forelimb length more closely, although not exactly, parallel body mass (Zihlman and Cramer, 1978; Jungers and Susman, 1984). This results in systematic differences in intermembral index (IMI), with bonobos having a longer hind limb relative to their forelimb -- an IMI of about 102, vs. about 106 for common chimpanzees, which do not differ from one another (first noted by Coolidge (1933), also see Zihlman and Cramer, 1978; Zihlman et al., 1978; McHenry and Corruccini, 1981; Jungers and Susman, 1984; Morbeck and Zihlman, 1989). This runs counter to the broader scaling pattern of IMI in African apes in general, in which increases in body size are generally associated with relatively longer forelimbs (Cartmill, 1974; Jungers and Susman, 1984). Perhaps because of their generally slightly smaller body size and their relatively longer

limbs, bonobos have been reported to generally have smaller joints than common chimpanzees, both absolutely and relative to bone lengths (Zihlman and Cramer, 1978; McHenry and Corruccini, 1981; Jungers and Susman, 1984; Morbeck and Zihlman, 1989). Bonobos have also been found to have slightly more curved phalanges, with less robust flexor sheath ridges — again, generally interpreted as more arboreal morphology (Susman, 1979; Stern and Susman, 1983; Susman et al., 1984; Stern et al., 1995).

Interpretations of morphological differences between bonobos and common chimpanzees have often been contextualized in hypotheses about the processes shaping human evolution, with bonobos held to have special relevance to early hominins. Early descriptions of bonobos were influenced by the idea that humans evolved by retaining juvenile ape-like characteristics, describing bonobos as true paedomorphs and suggesting that they may be closer to the last common ancestor of *Pan* and *Homo* than common chimpanzees (Coolidge, 1933). More recent authors also suggested that bonobos are the best modern candidate for a prototypical "pre-hominin" ancestor, citing their more "generalized" morphology (i.e., small size and less sexually dimorphic faces, teeth, and overall body size) and intermembral proportions and aspects of femoral morphology more closely resembling early hominins (Zihlman and Cramer, 1978; Zihlman et al., 1978). Others, however, have pointed out that the most parsimonious interpretation of bonobo—common chimpanzee morphological differences is that bonobos are more derived, not generalized, and that postcranial similarities between bonobos and early hominins are overstated (Latimer et al., 1981). It has also been noted that many morphological differences between bonobos and common chimpanzees (e.g., most of the scapular differences discussed above) seem to be the result of ontogenetic scaling, or the

extension or truncation of common growth allometries – often suggested to be the result of selection for reduced sexual dimorphism in general, since this is a byproduct of truncation of growth (Shea, 1983). However, many other differences (most notably differences in skull, trunk, and relative limb lengths) are not – in these aspects, bonobo overall body proportions do not match a single ontogenetic stage of common chimpanzees.

Thus, because of the complex patterns of body size variation in the genus *Pan*, researchers have had trouble attributing all species differences solely to the allometric effects that have been invoked to explain similar variation in great apes broadly (Jungers and Susman, 1984) or to ontogenetic scaling and paedomorphism (Shea, 1983). While there have been some suggestions, the causal factors of morphological variation between and among the species and subspecies of *Pan* are still incompletely understood.

Table 1.2 Key postcranial morphological differences between species and subspecies of Pan

Feature	Difference	Sources
Body mass	Bonobos weigh less than common chimpanzees in general (with substantial overlap).	Zihlman & Cramer 1978, McHenry & Corruccini 1981
	Bonobos and *P. t. schweinfurthii* in general are similar in weight; both are smaller than *P. t. troglodytes*.	Jungers & Susman 1984
	Gombe *P. t. schweinfurthii* are smaller than both bonobos and other *P. t. schweinfurthii.*	Morbeck & Zihlman 1989, Pusey et al. 2005, Carter et al. 2008
Body measurements	Bonobos have shorter bodies (head to fork length) than *P. t. troglodytes*, but are similar in body height (total length from head to heel).	Coolidge & Shea 1982
	Bonobos and *P. t. troglodytes* are similar in chest girth relative to body length, but are smaller in chest girth relative to body height.	Coolidge & Shea 1982
Limb lengths (absolute)	Bonobos and common chimpanzee subspecies do not differ in average hindlimb length within sexes. Bonobo males have shorter forelimbs than both *P. t. troglodytes* and *P. t. schweinfurthii* males, and females have shorter limbs than female *P. t. troglodytes*.	Zihlman & Cramer 1978, Jungers and Susman 1984
	Gombe *P. t. schweinfurthii* tend to have shorter limbs than both bonobos and other *P. t. schweinfurthii.*	Zihlman et al. 2008; Morbeck & Zihlman 1989
	Taï Forest *P. t. verus* and Kibale *P. t. schweinfurthii* are similar in femur and humerus length and exceed femur and humerus length of Mahale and Gombe *P. t. schweinfurthii*, which are more similar to each other.	Carlson et al. 2010
Limb lengths (size standardized)	Bonobo humerus, tibia, and femur are longer relative to their body size than those of Gombe *P. t. schweinfurthii*, and bonobo humerus and femur are longer relative to their body size than other *P. t. schweinfurthii.*	Morbeck & Zihlman 1989
Joints	Bonobos tend to have both absolutely and relatively (compared to limb lengths) smaller joints than common chimpanzees; absolute differences are more pronounced in males.	Zihlman & Cramer 1978, Morbeck & Zihlman 1989, McHenry & Corruccini 1981, Jungers & Susman 1984

Table 1.2 (continued)

Feature	Difference	Sources
Limb indices	Bonobos have relatively longer hind limbs/shorter forelimbs than all common chimpanzees (related to their differences in absolute limb lengths), but similar brachial and crural indices.	Zihlman & Cramer 1978, McHenry & Corruccini 1981, Jungers & Susman 1984
	Intermembral index (IMI) does not differ between any common chimpanzee subspecies.	Morbeck & Zihlman 1989, Jungers & Susman 1984, Zihlman et al. 2008
	Brachial and crural indices are similar between Gombe *P. t. schweinfurthii* and Taï Forest *P. t. verus*.	Zihlman et al. 2008
Cross-sectional properties	Taï Forest *P. t. verus* have more elliptical diaphyses than *P. t. schweinfurthii*, Mahale *P. t. schweinfurthii* tend to be most circular.	Carlson et al 2011
	Bonobo females differ from *P. t. schweinfurthii* and *P. t. troglodytes* in femoral shape, but there are no significant differences between males.	Carlson et al 2011
Shoulder	Bonobos tend to have shorter clavicles than common chimpanzees.	Zihlman & Cramer 1978, Jungers and Susman 1984
	Bonobos have absolutely smaller scapular length, breadth, and infraspinous width (but not supraspinous width) than *P. t. troglodytes*. Bonobos males have shorter scapulae than male *P. t. troglodytes* and *P. t. schweinfurthii*, but females do not. Bonobo scapulae are longer relative to their breadth than *P. t. troglodytes* scapulae.	Shea 1986
	Gombe *P. t. schweinfurthii* have shorter clavicles than other *P. t. schweinfurthii* and *P. t. troglodytes*, but don't differ from Taï Forest *P. t. verus* (within sexes).	Zihlman et al. 2008
Pelvis	Bonobos have a shorter ilium than *P. t. troglodytes* and *P. t. schweinfurthii*; ischium is similar in all three taxa except in female bonobos, which have shorter ischia than female *P. t. troglodytes*. Pubis length is shorter in bonobos than either *P. t. troglodytes* or *P. t. schweinfurthii*, except for in female bonobos and *P. t. schweinfurthi*i, which are similar.	Jungers and Susman 1984
	Taï Forest *P. t. verus* females have broader ilium, longer inominate, and larger acetabulum than Gombe *P. t. schweinfurthii* females; males have larger acetabulum.	Zihlman et al. 2008
	Gombe *P. t. schweinfurthii* have a shorter inominate than other *P. t. schweinfurthii*	Morbeck & Zihlman 1989

Table 1.2 (continued)

Feature	Difference	Sources
Hand and foot bone lengths and length proportions	Bonobos have less sexual dimorphism in absolute MC length, but are similar in length relative to body size	Susman 1979, Inouye 1992
	Bonobo and common chimpanzees have similar phalangeal length patterning (III>IV>II>V) and similar phalangeal length relative to size surrogate (humeral diaphyseal length).	Susman 1979, Inouye 1992
Metacarpal head morphology	Bonobo adults have more variably present and shorter DMR's than common chimpanzees.	Inouye & Shea 2004
	Bonobo metacarpal heads are absolutely longer and narrower than those of chimpanzees. However, relative to size surrogate (humeral diaphyseal length), bonobos have relatively smaller head widths.	Susman 1979, Inouye 1992
Metacarpal shaft dimensions	Bonobo metacarpal cortices absolutely thicker than those of common chimpanzees. However, relative to size surrogate (humeral diaphyseal length), bonobos have relatively smaller midshaft widths.	Susman 1979, Inouye 1992
Phalangeal curvature	Bonobo manual proximal phalanges are to be more curved than those of common chimpanzees, with substantial overlap.	Stern et al. 1983, Susman et al. 1984, Stern et al. 1995, Deane et al. 2008 (but see Jungers et al. 1997)
	Bonobo pedal proximal phalanges are slightly more curved than those of common chimpanzees, but the two are more similar than they are in the hand.	Susman et al. 1984, Stern et al. 1995 (but see Deane et al. 2008)

1.3.3 Behavioral variation in *Pan*

Given that morphological differences between bonobos and common chimpanzees cannot be fully explained by their size differences, a natural alternate explanation for these patterns of variation may be selection related to locomotion and positional behavior, which differs between *Pan* species and subspecies. However, attempts to link these factors have sometimes suffered from a paucity of sufficiently complete field data (or the complete absence of field data, as is the case for *P. t. troglodytes*), or problems with habituation of study groups. The following sections review the history and major findings of behavioral studies of adult common chimpanzees, adult bonobos, and the locomotor ontogeny of both taxa, with key quantitative studies listed in Table 1.3.

Table 1.3 Key quantitative locomotor behavioral studies of the genus Pan

Refence	**Study site**	**Taxon**	**Age range**
Doran (1989; 1992a; 1993)	Taï Forest, Ivory Coast	*P. t. verus*	Adult and ontogenetic
Doran (1989; 1992b; 1997)	Lomako Forest, Democratic Republic of Congo	*P. paniscus*	Adult and ontogenetic
Hunt (1989; 1992)	Mahale and Gombe, Tanzania	*P. t. schw.*	Adult
Ramos (2014)	Lui Kotale, Democratic Republic of Congo	*P. paniscus*	Adult
Sarringhaus (2013a; 2013)	Ngogo, Uganda	*P. t. schw.*	Adult and ontogenetic
Susman (1980; 1984)	Lomako Forest, Democratic Republic of Congo	*P. paniscus*	Adult

1.3.3.1 Adult common chimpanzees

Much of the field research on common chimpanzees (as well as bonobos) has focused on adults. Earlier studies were more qualitative or descriptive in nature, with some exceptions. In 1965, Goodall described *P. t. schweinfurthii* at Gombe as being between 50 and 70% arboreal, but seldom traveling in the trees except for during the rainy season (Goodall, 1965). Around the same time, Reynolds and Reynolds (1965) described *P. t. schweinfurthii* at another site, the Budongu Forest, as also spending an average of 50 to 75% of their time arboreally. However, it was not until later that quantitative descriptions of chimpanzee behavior became more common.

Doran (1989; 1993) used instantaneous sampling of positional behavior in adult males and females from a habituated community of *P. t. verus* from the Taï Forest in the Ivory Coast to examine sex differences in locomotion. There were no significant sex-related differences in overall percentage of time spent in any of the five locomotor categories she designated (quadrupedalism, quadrumanous climbing and scrambling, suspension, bipedalism, or leaping). However, when data were subdivided and only activities taking place on arboreal substrates were analyzed, she found that adult males tended to use less quadrupedalism and more quadrumanous climbing and scrambling than females. Males tended to spend more of their total time (i.e., combined resting and active locomotion) on the ground, with the exception of one month during which the chimpanzees preferred to eat a species of nut that could only be consumed terrestrially. However, consideration of only locomotor behavior results in much more similar frequencies between the sexes in time spent terrestrially, suggesting that most of this discrepancy in arboreal vs. terrestrial behavior between the sexes was driven by time

males spent resting on the ground (See Doran (1989), Ch. 4). This indicates that it is important to carefully consider whether behavioral frequencies are reported as percentages of total time or percentages of locomotor time only.

Hunt (1989; 1992) studied positional behavior in *P. t. schweinfurthii* at two sites: Mahale and Gombe, both in Tanzania. Instantaneous samples were recorded every two minutes on focal animals, along with various social, feeding, habitat, and substrate variables potentially related to behavior. A portion of the study also included collection of continuous samples of climbing bouts recording size and angle of substrate, height climbed, and type of climbing. Mahale is a closed forest, while Gombe is semi-deciduous, with substantial differences in ground cover between the two sites (Hunt, 1989). Positional behavioral categories included knuckle-walking, climbing, palmigrade walking, running, bipedalism, brachiation, and "other suspensory" behavior. Males were found to spend more time on the ground than females and to perform less palmigrade walking, climbing and arm-hanging. The aforementioned difference in knuckle-walking vs. palmigrade walking was only significant at Gombe, although both sexes of chimpanzees at this location were less terrestrial than those at Mahale (somewhat unexpected, given that Gombe is actually a more open environment). Continuous sampling of climbing bouts related to body size and social rank shows that, in the Mahale chimpanzees, there is an interaction between body size, social rank, and substrate preference that complicates what initially appear to be simple anatomical relationships between size and substrate diameter preference, although large males were found to be more terrestrial and climb less than smaller males regardless of rank (Hunt, 1995).

Comparison of the behavior of *P. t. schweinfurthii* at Mahale and Gombe with that of *P. t. verus* at Taï Forest reveals some basic differences between the three sites. Although all the chimpanzees spend the vast majority of their locomotor time in knuckle-walking quadrupedalism, males at Taï Forest appear to be more arboreal than males at the other two sites, while females at both Taï Forest and Gombe are more arboreal than females at Mahale. In keeping with this, overall frequencies of locomotor behaviors are somewhat different, with frequencies of arboreal-specific behaviors such as climbing and scrambling somewhat over-represented at Taï Forest compared to Mahale and Gombe (Doran and Hunt, 1994). When only the subset of locomotor behavior on arboreal substrates is considered, males and females at Mahale and Gombe do not differ from one another, but Taï Forest males use less quadrupedalism and more climbing than both Taï Forest females and Mahale and Gombe chimpanzees (which are more similar to each other, Doran and Hunt (1994)). There are also subtle differences in the way sex/population groups perform arboreal quadrupedalism: although they use it less commonly, Taï Forest males (and to a lesser extent, females) tend to prefer to knuckle-walk when engaging in quadrupedal behavior arboreally, while Gombe and Mahale chimps more frequently use palmigrade postures (Doran and Hunt, 1994). This may relate to differences in substrate use ultimately tied to habitat, as Taï Forest chimpanzees also use more substrates of either extremely large (trunks) or small (liana and foliage) diameter, rather than the mid-size boughs and branches more frequently used by Mahale and Gombe chimpanzees (Doran and Hunt, 1994).

Some of the observed locomotor differences may be size-related. While relationships between body mass, environment, and other social factors are complex,

some studies have demonstrated an inverse relationship between body size and climbing, finding that larger male chimpanzees are less likely to be found at high levels in trees than smaller males (Hunt, 1995). Alternatively, or additionally, they may also be due to the habitat differences between sites and subspecies (see Genetic and Ecological Variation).

Generally, however, common chimpanzees are broadly similar to one another in overall behavioral frequencies as adults, with slight variation both between and possibly within subspecies. These differences are most pronounced in relative frequencies of quadrupedalism vs. climbing and scrambling behavior, which vary between *P. t. verus* and *P. t. schweinfurthii*, possibly within some populations more than others.

1.3.3.2 Adult bonobos

Locomotor behavioral studies of *P. paniscus* began slightly later than studies of *P. troglodytes*. Again, initial efforts were generally descriptive and qualitative, with some exceptions. Horn (1976; 1980) attempted an initial study of bonobos at Lake Tumba, but the group was unhabituated and difficult to observe. He suggested that they spent a large amount of time on the ground, and that they preferred to climb up sloping branches rather than suspend themselves by their arms to ascend into or move about on arboreal substrates. In contrast, Kano (1983) observed bonobos at Yalodisi moving horizontally in trees using either knuckle-walking or palmigrade quadrupedalism, and traveling between trees by pulling themselves across the gaps (although he also noted that suspensory behaviors were less common). Badrian and Badrian (1977) also concluded that bonobos were more arboreal than common chimpanzees.

Most quantitative (and some qualitative, as mentioned above) field studies of bonobo locomotor and postural behavior have been limited by incomplete habituation, which may impact locomotor behavior frequencies. In a pair of studies on the Lomako bonobo population, the initial study found a high frequency of diving and leaping; however, data from the same population several years later showed a decrease of almost 10% in the frequencies of these behaviors that was attributed to increased habituation of the bonobos at the site (Susman et al., 1980; Susman, 1984). Habituation may also impact frequency of arboreal behavior in particular: at Wamba, pre-habituated bonobos fled from observers in trees, but post-habituated bonobos traveled mainly terrestrially (Doran, 1996). In general, based on these observations, less habituated bonobo populations could be expected to have higher frequencies of avoidance and fleeing behaviors such as leaping or other potentially risky arboreal maneuvers, as well as spending more time arboreally in general.

In fact, for the majority of quantitative behavioral studies of bonobos, lack of habituation meant that the groups could not be reliably observed terrestrially at all. Thus, while complete arboreal and terrestrial data are available across multiple sites in common chimpanzees, most *P. paniscus* behavioral data are restricted to arboreal substrates. Studies have generally found that, in arboreal behavioral frequencies, quadrupedalism was the most common, followed by climbing and scrambling and leaping/diving, with relatively low frequencies of bimanual suspension and bipedalism (Susman et al., 1980; Susman, 1984; Doran, 1996). These studies have also noted that terrestrial quadrupedalism was fairly frequent, although as stated above, terrestrial behavior could not be observed reliably enough to collect quantitative data. In general, therefore, earlier

studies comparing bonobo and common chimpanzee behavior have indicated that the two differ substantially in their arboreal behavioral repertoires, with bonobos having higher frequencies of leaping and a tendency towards suspensory, rather than climbing, behavior, especially in comparisons between males (Doran and Hunt, 1994; Doran, 1996). Both male and female bonobos preferred palmigrade to knuckle-walking quadrupedalism more frequently, but they are more similar to *P. t. schweinfurthii* in this regard than to Taï Forest *P. t. verus* (Doran and Hunt, 1994).

However, recent data on adults from a different, more completely habituated bonobo population differ substantially from these earlier studies, showing marked similarity in overall locomotor profiles between bonobos and common chimpanzees, with less arboreal leaping and suspensory behavior in bonobos (Ramos, 2014). This is somewhat more consistent with observations that bonobos may rely significantly on terrestrial herbaceous food sources (Malenky and Wrangham, 1994), but is less consistent with interpretations of bonobo morphology hinging on locomotor paedomorphism. It also raises questions about the nature of ontogenetic locomotor change in bonobos (see below).

It is possible that these new results either represent population-level variation within bonobos or are an artifact of methodological differences between studies (data collection methods, observer effects, differences in data pooling, etc.). However, these explanations seem less likely in view of the known incomplete habituation in the earlier data set, and the fact that the behavioral differences between bonobo populations differing in degree of habituation resemble the differences observed in a single population that increased in habituation over time (Susman et al., 1980; 1984).

1.3.3.4 Bonobo and common chimpanzee locomotor ontogeny

While the vast majority of research into positional behavior in chimpanzees has focused on comparisons of adults, some have also presented data on the way these behaviors change during ontogeny. Early texts by Goodall (Goodall, 1965) reported that infants, juveniles and young adolescents at Gombe moved quickly in arboreal settings, but that with age they began to be more cautious and move more slowly.

The first systematic, quantitative documentation of chimpanzee locomotor ontogeny was performed on the Taï Forest population of chimpanzees. (Doran, 1989; 1992b; 1997). *P. t. verus* were found to change in locomotor behavior with age, becoming more terrestrial and quadrupedal and less arboreal and suspensory. Knuckle-walking quadrupedalism also increased in frequency as individuals acquired more adult-like locomotor patterns. The rate of change was not constant, showing relatively drastic increases in quadrupedalism in infancy, especially after about two years of age, plateauing later in life. Quadrupedalism was found to be the predominant locomotor behavior shortly after infants crossed the two year age boundary, with basically adult-like levels reached by juvenility, when animals were traveling and resting independently of their mothers (Doran, 1992b). These were the only available ontogenetic locomotor data for *P. troglodytes* for many years, and this pattern was sometimes assumed to be common to all common chimpanzees. However, a recent study of locomotor behavior ontogeny in *P. t. schweinfurthii* from Kibale (Sarringhaus et al., 2013) suggests that there may be slight differences in locomotor ontogeny between common chimpanzee subspecies or between sites: while chimpanzees in this population do decrease in arboreal and suspensory behavior with age, they appear to do so at a more gradual rate than in the Taï

Forest population. In the Kibale chimpanzees, quadrupedalism does become the most common locomotor mode by juvenility, around 5 years of age, but frequencies of quadrupedal behavior continue to increase through adolescence (Sarringhaus et al., 2013), marking juvenility as a more transitional period between infancy and adulthood and suggesting overall more gradual rates of ontogenetic locomotor change. While some of this appearance may be due to methodological differences between the two studies (age categories are more granular in the later study, allowing for finer resolution of ontogenetic patterns, and locomotor categories are slightly different, having been more explicitly designed to isolate fore- and hind limb loading behaviors), the differences persist even after these have been factored in (see Methods). These patterns of variation could again ultimately relate to habitat differences and have sometimes been suggested to relate to tree height and density at different sites (although this does not always explain differences; Doran and Hunt, 1994; Sarringhaus et al., 2013).

Doran (Doran, 1989; 1997) was also the first to quantify *P. paniscus* locomotor ontogeny, studying bonobos at Lomako. As with studies of adult bonobos, behavioral data were difficult to collect on juveniles, so comparisons were again restricted to arboreal behaviors only for *P. paniscus*. Even when using arboreal substrates, like common chimpanzees, bonobos were found to change in locomotor behavior with age, becoming less suspensory and more quadrupedal (Doran, 1989; 1992b). However, while basic patterns were the same, bonobos changed less, and juveniles and adolescents were more suspensory than common chimpanzees in the same age categories — in fact, bonobo adults were actually found to be most similar to older infant *P. t. verus* in their overall arboreal behavioral patterns (Doran, 1992b).

Based on these data, bonobos were described as "locomotor paedomorphs", with adult behavioral profiles resembling those of immature common chimpanzees, and experiencing overall less ontogenetic change in positional behavioral frequencies; this was suggested to relate to their morphological paedomorphism, as discussed above (Doran, 1993). However, this picture is complicated somewhat by more recent studies, most notably Ramos (2014). Although to date, there are no ontogenetic locomotor behavioral data for bonobos that are not affected by the incomplete habituation, preliminary unpublished data (collected for a study of tool use) suggest that immature bonobos from age 1-7 may be as much as 80% arboreal on average (although likely somewhat lower; Dr. Kathelijne Koops, pers. comm.). If this is accurate, and if previous findings of less age-related change in bonobos were due to abnormally high degrees of suspension and arboreality in adults (as suggested by Ramos (2014)), then they may actually experience decreases in arboreal behavior similar to those observed in common chimpanzees. Further behavioral data are needed to explicitly demonstrate this effect.

From this body of research, it seems likely that there is a common pattern of decreases in arboreal behavior in the genus *Pan* throughout ontogeny. In contrast to some other primates (e.g., *Gorilla beringei beringei*, Doran (1997)), this decrease occurs relatively gradually. However, it is also clear that there are likely species, subspecies, or even population differences in behavioral ontogeny in *Pan*, the degree and causation of which are still incompletely understood.

1.4 BONE MORPHOLOGY AND PLASTICITY

1.4.1 Differential plasticity of skeletal structural properties

Articular surfaces are important both in weight transfer and in determining the range of motion and the stability of a joint (Ruff, 1988; Godfrey et al., 1991; Rafferty and Ruff, 1994). Their external dimensions vary systematically across primates along broad locomotor patterns: for example, relatively larger femoral and humeral heads in hominoids may relate to their use in more variable limb positions (Ruff, 1988; 2002; Hammond, 2014). Articular cartilage is responsive to compressive loading (Meikle, 1975), and stress across an articular surface is (broadly) a function of applied force relative to its surface area (Biewener, 1989). Joints can and probably do respond to forces across the opposing surfaces during growth, which help to guide proper development (Hamrick, 1996; 1999), so articular size might be expected to increase with increased activity and loading. However, there is little to no experimental support that changes in load magnitude affect articular size, especially after epiphyses fuse (Lieberman et al., 2001), although other aspects of articulations such as trabecular architecture and subchondral bone density are more so (Rafferty and Ruff, 1994; Pontzer et al., 2006; Patel and Carlson, 2007). This apparent developmental constraint on external dimensions makes intuitive sense, because articular surfaces are also functionally constrained by the need for congruence with the opposing joint.

While absolute bone lengths are sensitive to environmental variables such as nutrition (Tanner et al., 1982; Serrat et al., 2008), limb bone length proportions are another aspect of skeletal morphology that appears to be primarily genetically determined (although interestingly, recent research in non-primates suggests that there may be a

degree of prenatal phenotypic plasticity in limb length proportions related to embryonic movement, Pollard et al. (2017)). In primates, fore- to hind limb length ratios in adults track broad locomotor behavior differences (Schultz, 1937; Fleagle, 2013). Relatively longer forelimbs are generally associated with forelimb-dominated climbing and suspension (Jungers, 1985; Godfrey et al., 1991; Ruff, 2002), and relatively longer hind limbs with leaping behavior (Connour et al., 2000). Experimental studies suggest that limb lengths are not altered by increases in loading (Lanyon, 1980), and this interpretation is supported by evidence from a variety of taxa (Carrier and Leon, 1990; Ruff, 2003a; Auerbach and Ruff, 2006). Evolutionary time is required for length proportions to change: recent studies show that adult mountain (*Gorilla beringei beringe*i) and lowland gorillas (*Gorilla gorilla gorilla*), which likely diverged from one another between 0.5-2mya (Langergraber et al., 2012; Prado-Martinez et al., 2013), show no differences in fore- to hindlimb length proportions despite substantially lower arboreal substrate use in the former (Ruff et al., 2013). Because length proportions are relatively insensitive to (non-pathological) loading during life but seem to correlate well with behavior at broad scales, they likely are genetically constrained, reflecting long-term evolutionary adaptation rather than (necessarily) the current loading regime.

In contrast to articular size and limb proportions, other structural features seem to be more developmentally plastic. The idea that bone changes to adapt to mechanical loads upon it (sometimes termed "Wolff's law", although there are some issues with this terminology (Ruff et al., 2006)) has been the focus of many studies. This remodeling appears to be in response to strain (not stress), although the proximate causes of the bone response are still being explored (Currey, 2002). The relationship is generally

characterized as a feedback model, wherein bones are modified either by resorption or deposition of bone tissue in order to keep strains within an "optimum" or customary window (Frost, 1987; Turner, 1998). Several classic studies have added additional detail about the nature of this process. Both bone geometry and bone material properties such as mineralization, porosity, and collagen fiber orientation are important in determining bone strength (Currey, 2002), but bone primarily responds to loading by altering its geometry (as measured by cross-sectional properties) (e.g., Robling et al. (2002), Kontulainen et al. (2002)). Bone material properties appear to change less; in fact, unlike geometry, bone mineral properties are actually fairly constant (in adults) even across extremely large taxonomic ranges (Erickson et al., 2002). Because the bony response is dependent on the magnitude and frequency of applied strains, dynamic activities are more important in generating these changes in geometric properties (Rubin and Lanyon, 1982; Turner, 1998; Ruff et al., 2006). The degree of osteogenic reaction is also, to some extent, dependent on age: bone responds much more dramatically to loading in younger individuals (Forwood and Burr, 1993; Turner and Robling, 2003), although loading still alters bone geometry in adults, given enough time (Kerr et al., 1996; Valdimarsson et al., 2005). Reduced activity in adulthood also seems to result in the loss of some of the bone built up during the juvenile period (Pearson and Lieberman, 2004). Bone may also respond differently in young children and adolescents than it does in adults, with the former group primarily exhibiting increases in strength via expansion at the periosteal surface and the latter increasing in strength primarily due to endosteal contraction (Ruff et al., 1994).

Links between bone geometry and loading have now been well documented in a variety of taxa, including both human and nonhuman primates (Ruff and Runestad, 1992; Biewener and Bertram, 1994; Bass et al., 2002). Much of this work has been on the diaphysis. Recent research has also focused on functional signals in trabecular bone, although its relationship with behavior appears to be somewhat complicated, at least with currently used parameters (Ryan:2009ff; also see Keaveny et al., 2001; Pontzer et al., 2006; Patel and Carlson, 2007; Ryan and Walker, 2010).

Because of these functional links between bone diaphyseal strength and loading, various studies have suggested that inter- and intra-limb ratios of cross-sectional strength contain information about relative limb usage. Writ large, this seems to be the case: relative strength of the forelimb compared to the hind limb bones differs between broad locomotor categories of primates and other animals distinguished by different limb usage patterns (Schaffler et al., 1985; Demes and Jungers, 1993; Ruff, 2002; Habib and Ruff, 2008). Intra-limb ratios of bending strength and rigidity may also contain functional information: the robusticity of the fibula relative to the tibia appears to distinguish positional behavioral categories in hominoids (Marchi, 2007), as does the cross-sectional geometry of hand and foot metapodials (Marchi, 2005; Byron et al., 2015). There is also some suggestion that ulnar to radial strength ratios may relate to hand posture in knuckle-walking primates, although this remains to be tested systematically (Ruff et al., 2013).

Internal shapes of bone cross sections may also contain information about loading, because higher or more stereotypical strains in a particular plane may be expected to result in preferential strengthening of the bone in that plane. These are generally quantified using ratios of bending rigidity or strength in orthogonal planes,

either anteroposterior and mediolateral (Ix/Iy or Zx/Zy) or the maximum and minimum (Imax/Imin) for the bone. For example, an increase in anteroposterior strains in horse metacarpals are associated with higher ratios of A-P to M-L bending rigidity (Nunamaker et al., 1989), and cross-sectional shape also appears to relate to activity levels in humans (Ruff, 1987a; Stock and Pfeiffer, 2001). Shape ratios may also be informative about arboreal clambering behavior (which tends to load the limb in a varied, non-stereotypical manner) across broad categories of primates (Carlson, 2005), but these relationships are less consistent within subspecies or at the individual level (Carlson et al., 2006; 2008; 2010). Recent studies have developed new methods of quantifying cortical shape continuously within bone cross sections, rather than using shape ratios, and have also found links with behavior (Jashashvili et al., 2015).

However, interpretation of cortical bone morphology is complicated by several factors. Most notably, the "optimum" strain windows for each bone may be under some degree of genetic control and/or be impacted by systemic factors like age or hormone levels, as well as differing along the limb (Lieberman et al., 2003; Ruff et al., 2006). The degree to which bone cross-sectional geometry is influenced by these factors (Lovejoy et al., 2003; Peacock et al., 2005; Prentice, 2007) complicates the strength and nature of its relationship to behavior during life. At a minimum, this suggests that comparisons should be restricted to relatively closely related taxa to avoid confounding genetic and direct behavioral effects. The amount of evolutionary time or genetic difference needed to have an appreciable effect on morphology is also still unclear, although this can be difficult to separate from general correlations of locomotor differences with time of separation between groups (Blomberg et al., 2003).

Because the hands and feet are the parts of the appendicular skeleton that actually contact the substrate during locomotion, they may be expected to be as sensitive to loading, if not more so, than the more proximal limb bones. In addition to the cortical and trabecular bone parameters discussed above, external characteristics of the hand and foot bones have also been argued to relate to behavior in primates.

Phalangeal curvature has been associated with arboreal behavior for many years (reviewed in Stern et al., 1995). There have been several proposed functional explanations for phalangeal curvature. Some authors have argued that curved phalanges reduce muscular effort necessary to resist loading (Preuschoft, 1971), or that they allow more contact between skin and substrate and increase the diameter of the support that a digit of a given length is able to grasp (Hunt, 1991). Other authors argued that phalangeal curvature reduces bending stress and strain during grasping with flexed digits (Oxnard, 1973; Preuschoft, 1973a; b; 1975), a hypothesis that was supported by finite element modeling, which showed that a curved phalanx loaded in suspension experiences less than half the strain of a straight phalanx of equal length at equivalent locations (Richmond, 2007). There have been several proposed methods for quantifying curvature (Stern et al., 1995; Deane and Begun, 2008), which sometimes give different results (Deane and Begun, 2008; Alba et al., 2010; Deane and Begun, 2010). However, regardless of method, curvature varies across primates with degree of arboreality, with more suspensory taxa having more curved phalanges than less suspensory taxa (Stern et al., 1995; Jungers et al., 2002; Deane and Begun, 2008; Rein, 2011).

Less attention has been paid to metacarpal and metatarsal curvature, although where discussed, it has generally been assumed to have similar functional interpretations

and be produced by the same processes (Harmon, 2013). Recently, however, metacarpal curvature in apes has been argued to relate instead to knuckle walking behavior. In long bones generally, it has been proposed that when bones are primarily loaded in bending, bone curvature increases the predictability of force distribution along the bone diaphysis (Biewener, 1983; Biewener and Bertram, 1994). Long bones are variably curved both between and among different animals, and patterns of curvature have sometimes been proposed to relate to functional demands of particular behaviors (Swartz, 1990). Normal curvature only develops in the context of normal loading (Lanyon, 1980). Knuckle walking is relatively unique among primate hand postures in the loading it produces on the metacarpals, which are positioned almost perpendicular to the substrate (in contrast to many other types of locomotion, in which the metacarpals are more parallel; Susman, 1979). Qualitative differences in metacarpal curvature have been noted among hominoids (Susman, 1979), and while few quantitative studies exist, there do seem to be some differences in metacarpal curvature between taxa consistent with differences in knuckle-walking behavior, with higher curvature found in metacarpals of adult knuckle-walking African great apes than in those of suspensory Asian apes (Sarringhaus, 2013a).

The identification of skeletal features specifically indicative of knuckle walking behavior has been an important task for students of human evolution. This is because there has been long-standing and vigorous debate over the nature of the locomotor behavior from which bipedalism in hominins originated. There are two main models: one in which the last common ancestor was a terrestrial knuckle-walker, and one in which this ancestor was a generalized arboreal climber (reviewed in Richmond et al., 2001). These models also inform, and are informed by, two competing ideas about the evolution

of knuckle-walking behavior in hominoids: namely, whether knuckle-walking evolved once, in the last common ancestor of chimpanzees, gorillas, and humans, or whether it evolved in parallel in chimpanzees and gorillas (Richmond et al., 2001). Knuckle-walking is kinematically and biomechanically distinct from other forms of locomotion and differs subtly between chimpanzees and gorillas (Tuttle, 1967; Inouye, 1989; 1994a; Matarazzo, 2013), and there have been many skeletal features in the wrist and hand purported to relate specifically to knuckle-walking behavior (Dainton and Macho, 1999; Inouye and Shea, 2004; Orr, 2005; Kivell and Schmitt, 2009). However, many of these features, especially in the wrist, have subsequently been found to be quite variable (despite supposed behavioral homogeneity), and are also often found in non-knuckle-walking taxa (Kivell and Schmitt, 2009).

In the hand, dorsal expansion of the articular surface of the heads of the metacarpals (dorsal metacarpal ridge, or DMR) has been argued to help maintain the typical hand posture used in knuckle walking by preventing hyperextension of the metacarpophalangeal joint (Tuttle, 1967; 1969). However, the ridge is variably present in adult African apes (despite frequent knuckle-walking in all taxa; Inouye (2004)). Ridges are more common in adults than in immatures (see below). Ridge height differs between male and female gorillas and is positively allometric with respect to size, with relative ridge height in gorillas matching what would be expected for a chimpanzee of comparable size (Inouye and Shea, 2004). This suggests that this feature is predominately related to body size rather than being strictly necessary for knuckle walking (although it is likely related to knuckle walking as well; Inouye and Shea, 2004). Instead of ridge height, the angle between the dorsal metacarpal surface and the articular surface of the

ridge may be a better proxy for knuckle-walking: it does not differ between males and females or between adult male gorillas and chimpanzees (although it still differs between adults and juveniles, see below, Sarringhaus (2013a)).

Generally, although the plasticity of some aspects of the skeleton has been well documented, the degree to which it is reflective of relatively fine-grained behavioral differences among very closely related taxa is still not clear — an especially important issue in interpreting the morphology of fossil hominins, for the reasons already discussed.

1.4.2 Ontogeny as a "natural experiment"

These issues can be clarified by using ontogenetic studies as a means of refining our understanding of the relationships between morphology and behavior and the developmental plasticity of long bone structural features — an area of study in which there has been increasing interest. Ontogenetic patterns can help to identify when and how differences between taxa arise in the context of developmental transitions during life, and ontogenetic studies can serve as "natural experiments" to test associations between changing locomotor behavior and skeletal morphology while naturally controlling for the effects of phylogenetic heritage. This is especially true when analyses explicitly include chronological age, either estimated or known, rather than using size measurements as the baseline for assessing developmental changes. Chronological time is important in development: not all ontogenetic changes are linear, so size cannot be a substitute for time (Klingenberg, 1998). Therefore, to extract the full benefit from ontogenetic analyses, it is useful to consider morphology with respect to behavioral changes in a chronological framework (especially when comparing directly to ontogenetic behavioral change, which is also not necessarily linearly related to size).

Considering adult locomotion and skeletal systems in the context of their development is also an important practice in and of itself. Although mechanical loading during adulthood does affect morphology, bone is most responsive to loading during the growth period, as discussed above. Adult bone is therefore likely to be reflective not only of adult (or immature) loadings, but rather, a mixture of both. Also, because immature animals are both more likely to be targets of predators and less experienced at negotiating their environments, it is likely that the adult locomotor skeleton is at least partially reflective of adaptation for success as juveniles — selection does not act only on adults (Carrier, 1996). Immature animals are also smaller than adults and have weaker bones and muscles (see below), but have to negotiate the same environments, which may require that juveniles be different in proportion from adults (Carrier, 1983). As animals mature, there exists tension between the extent to which they adapt their changing morphology to produce similar locomotor patterns, or change their locomotor patterns in conjunction with proportional change (Turnquist and Wells, 1994).

In some cases, skeletal proportional changes seem to drive locomotor changes, particularly in relation to gait kinematics. Ontogenetic change in limb length proportions has been tied to shifts in preferred gait patterns in maturing macaques and squirrel monkeys as they acquire more characteristically "adult" (and characteristically "primate-like") predominately diagonal sequence, diagonal couplet gait patterns (Shapiro and Raichlen, 2005; 2006; Young, 2012). Because these changes are not associated with either age or body mass, it seems unlikely that they are related to neuromuscular maturation — instead, they are likely responses to "lower-level" biomechanical factors (Young, 2012). While there is still debate over exactly what these might be, these studies

do show that ontogenetic change in locomotor kinematics is, in some cases, directly associated with changes in limb structural properties.

However, while limb lengths may alter gait kinematics, they are not as directly tied to locomotor behavior broadly. Infant galagos have not yet reached adult-like intermembral or trunk to limb length proportions at the onset of independent locomotion (Schaefer and Nash, 2007), and in humans, changes in length proportions and behavioral shifts from crawling to walking are also not strongly associated (Ruff, 2003a). This does not mean that length proportions are constant during ontogeny: infant gorillas show marked shifts in inter-limb proportions just after birth, with rapid attainment of higher intermembral indices/relatively longer forelimbs occurring prior to significant amounts of independent locomotion, suggesting this is not a meaningful factor driving these changes (Ruff et al., 2013). This is the opposite of growth patterns in sifakas, in which infants begin with slightly higher intermembral indices than they possess as adults (Ravosa et al., 1993). In both cases growth trajectories in limb length eventually produce inter-limb proportions that are adaptive for that species' form of locomotion, i.e., hind limb dominated vertical clinging and leaping in sifakas versus knuckle-walking and forelimb dominated climbing in African apes. While it therefore seems that growth trajectories for limb lengths clearly relate to behavior in some ways, these trajectories do not appear to be responsive directly to specific behavioral shifts. Rather, they may be more genetically determined/canalized, as discussed above, and subject to longer-term evolutionary pressures (also see Young et al. (2010b)). However, while large-scale evolutionary and commensurate large-scale behavioral differences may ultimately drive major changes in limb length proportions, the effects of more subtle behavioral variation between closely

related taxa have not been as well studied and may be clarified through ontogenetic comparisons.

Despite the well-documented links between bone diaphyseal cross-sectional properties and loading in adults, relatively few studies have examined the development of cross-sectional geometry. In humans, the characteristic relatively strong lower limb only appears around the age of the onset of bipedal walking after one year of age, and the midshaft of the femur changes in shape in conjunction with reduction in mediolateral forces with the attainment of mature bipedal gait at around age five (Ruff, 2003a; Cowgill et al., 2010). In contrast, baboons, which are terrestrial quadrupeds throughout their maturation, do not show similar drastic changes in strength proportions (Ruff, 2003a), although they too may change in cross-sectional shape in relation to limb posture (Burgess et al., 2016). Mountain gorillas, which decrease drastically in arboreal behavior at around age two (Doran, 1997), experience a concurrent drastic decrease in relative forelimb strength: before age two, they are similar in forelimb strength to adult lowland gorillas, which are more arboreal (Ruff et al., 2013).

As noted above, two separate studies have documented decreases in forelimb loading behavior with age in common chimpanzees, although there may be some population or subspecies-level differences in the degree and timing of these shifts. *P. troglodytes* in general also show increases in femoral strength and decreases in humeral strength with age (Sarringhaus and MacLatchy, 2016) consistent with behavioral data. This is especially true for *P. t. schweinfurthii* at Ngogo, where behavioral categories were explicitly designed to capture variation in predominantly forelimb vs. predominantly hind limb loading behaviors with the aim of comparing to limb bone structural properties

(Sarringhaus et al., 2013). Limb bones were also found to change in shape, with the femoral diaphysis becoming more elliptical with age, suggested to be related to more stereotypical, predominantly AP loading associated with increasingly high frequencies of terrestrial quadrupedalism (Sarringhaus and MacLatchy, 2016). This study suggests that in chimpanzees, as in other primates and apes in particular, limb bone structural properties do reflect ontogenetic locomotor change (although how sensitive these are to very subtle subspecies-level behavioral and genetic differences is still unclear; see below).

Not all studies have reached similar conclusions. Morimoto et al. (2012; 2014) compared phenotypic variation in morphometric maps of cortical bone in the femoral diaphysis to genotypic variation in chimpanzees and bonobos at different ages. They found that genotypic and phenotypic data were most highly correlated at young ages, with correlations decreasing in older individuals and adults. This was interpreted to mean that initial morphological variation reflects a neutral state rather than taxon-specific adaptation, and that subsequent changes are caused by taxon-specific genetic programming. This interpretation is largely based on the assumption that environmental variance remains constant over time (Morimoto et al., 2011). However, because changes in behavior and therefore loading have been documented for several of these taxa, it seems clear that the loading environment does not remain constant; an alternate interpretation for these results is that environmental variation does contribute to the phenotype and this contribution builds with age. Other studies have also found early similarity with subsequent divergence of ontogenetic trajectories of limb bone cross-sectional geometry in captive and wild *G. g. gorilla*, which seems to indicate

environmental effects rather than genetic programming (Canington et al., 2017). Regardless, these studies show that complex relationships between genotype, phenotype, and environment can be elucidated by examining their relationships over developmental time.

In considering the ontogeny of cross-sectional properties, it is also important to take into account the fact that bone material properties change with age (in contrast to comparisons across adults, when material properties are assumed to be similar; see above). Young juvenile bone is less mineralized than adult bone (Torzilli et al., 1982; Heinrich et al., 1999), but still needs to function in locomotor activities. Bone geometry generally scales negatively allometrically during ontogeny, such that younger animals have relatively stouter bones for their body size (Carrier, 1983; Carrier and Leon, 1990; Heinrich et al., 1999; Main and Biewener, 2007). It is commonly proposed that this negatively allometric scaling of cross-sectional area across ontogeny is a product of geometrical compensation for weaker bone tissue early in development (Carrier and Leon, 1990). This pattern of increased geometric robusticity and reduced stiffness due to incomplete mineralization increases the work to fracture of immature bone, leading to larger safety factors in younger individuals (Main and Biewener, 2006). This arguably allows juveniles to engage in locomotion without undue risk of bone fracturing. This scaling phenomenon has rarely been studied in primates, but capuchin monkeys follow the trend of negative allometry, both in limb bones and in caudal vertebrae (Young et al., 2010a; Russo and Young, 2011). However, because bone lengths grow with positive allometry, bones are actually strongest relative to bending loads (which should be proportionate to body mass*bone length) at infancy and decline subsequently (Young et

al., 2010a). Thus, it is important to consider relative geometric strength independently for each bone to clarify the causes of change in proportions.

Patterns of ontogenetic change in aspects of hand and foot morphology have helped to clarify the nature of their relationships with behavior. Relative phalangeal length compared to metacarpal and metatarsal length declines with age in capuchins, due primarily to extended durations and faster rates of growth in metapodials — this has been suggested as evidence for selection for improved grasping ability in infancy, although again, it is not associated in time with specific behavioral transitions (Young and Booth, 2016). Although some phalangeal curvature is evident pre-birth, suggesting a genetic component, curvature declines with age in taxa experiencing some behavioral change (*G. g. gorilla*, *M. mulatta*, and *P. troglodytes*, although quantitative data are not available for all). This change is not found in orangutans and gibbons, which remain more arboreal in behavior across ontogeny. This has been interpreted as supporting evidence for a strong causative relationship between arboreal behavior and phalangeal curvature from cross-taxon comparisons (Paciulli, 1995; Richmond, 1998). The dorsal metacarpal ridge also becomes more prominent with age in gorillas and chimpanzees, but because ridge height is so strongly associated with body size in adults and does not correlate with locomotor transitions (at least in chimpanzees, Sarringhaus (2013a)), it is probably better interpreted as a body-size driven response to this kind of loading, as discussed above (Inouye and Shea, 2004). Of course, locomotor behavior is not independent of body size, so this may still be viewed as an example of developmental plasticity. Dorsal metacarpal ridge angle also becomes sharper with age and size, which has been suggested to be a response to knuckle walking (Sarringhaus, 2013a). Further study will clarify these relationships.

It is important to note in this regard that the relationships between skeletal morphology and locomotor behavior and habitat use are strongly mediated by body size. Some species of macaque pass through a transitional arboreal phase, which begins when they attain adult limb proportions at about 18 months of age and lasts until they reach adult body size, when they become more terrestrial. During this transitional period, they have attained the full potential of their locomotor system, but do not yet have the limits adult body size can place on the types of substrate that are usable (Wells and Turnquist, 2001). Chimpanzees and mountain gorillas perform similar frequencies of arboreal behavior when they are at the same body size, even though at these points they are at radically different ontogenetic stages (Doran, 1997). Kinematic and behavioral data show that adult gorillas, especially males, have more difficulty in climbing, and male lowland gorillas use arboreal substrates differently than females as a result of this (Remis, 1995; 1998; 1999; Isler, 2005). Large male chimpanzees use different tree heights and substrate diameters than small male chimpanzees from the same groups (when social rank is accounted for, Hunt (1995)). All this suggests that during growth, animals may pass through periods when arboreal environments are more accessible to them by virtue of a combination of limb proportions and body sizes. Therefore, interactions between limb proportions and body size are also important to consider in ontogenetic studies.

1.5 RESEARCH DESIGN AND HYPOTHESES

While some of the morphological differences between bonobos and common chimpanzees can be explained by ontogenetic extrapolation and/or scaling patterns across apes in general (Shea, 1986), as discussed above, others (specifically relative limb lengths) cannot. Given this, it is natural to attempt to functionally associate differences in

bonobo morphology with environmental or ecological parameters. Until recently, the available data have suggested that bonobos are more arboreal and/or more active in trees than *P. troglodytes*, are behaviorally more similar to immature *P. troglodytes* than they are to adults, and show less behavioral change with age. Many functional interpretations have therefore been based on the idea of bonobos as "locomotor paedomorphs" (see above). However, recent studies have called these previous behavioral data, and by extension interpretations of morphology based on those data, into question. The extent to which bonobo locomotor behavior resembles or does not resemble that of different subspecies of common chimpanzee is therefore still unclear, although differences may be less extreme than previously supposed.

One area that remains relatively unexplored is the ontogeny of bone structural properties at the subspecies level, especially with specific reference to chronological age. The studies discussed above suggest that different long bone morphological features are sensitive to behavioral variation at different evolutionary timescales. However, our current knowledge regarding intra-generic variation in the ontogeny of long bone structural properties in African apes is limited to *Gorilla* (Ruff et al., 2013). Patterns of ontogenetic change in long bone structural properties in the different gorilla species and subspecies have proven to be effective in identifying functional and phylogenetic correlations, but it is possible that these patterns may differ in bonobos and common chimpanzee subspecies, which have a different evolutionary history and divergence times (Prado-Martinez et al., 2013). In addition, if inter-limb ratios of cross-sectional properties can be shown to correlate with behavior in African apes more generally, then their ontogenetic patterning in bonobos may help to address ongoing debates about the nature

of bonobo locomotor ontogeny. In the absence of behavioral data, ontogenetic change in morphology that closely tracks behavior in taxa for which both types of data are available can then be used to generate testable predictions for bonobo behavioral ontogeny.

While some aspects of variation in postcranial morphology in bonobos and common chimpanzee subspecies have been well studied, especially in adults (as discussed above), a complete documentation of ontogenetic patterning of multiple functionally linked postcranial morphological characteristics in the genus *Pan* at the subspecies level is still lacking. This is especially true for bonobos, in which the ontogeny of morphology other than bone lengths tends to be relatively poorly characterized compared to common chimpanzees. Carlson (2005; 2008; 2010) showed that the shape of femoral and humeral cross-sections correlated with overall degree of arboreal behavior across adult great apes, but was less effective within taxonomically narrower groupings, and bonobos and common chimpanzees had relatively few differences. However, these studies did not explicitly compare between limbs or contextualize results with regard to relative forelimb and hindlimb usage. Fore- to hindlimb strength ratios have been shown to correlate with ontogenetic transitions to increased terrestriality in both mountain gorillas and one subspecies of common chimpanzee (Ruff et al., 2013; Sarringhaus and MacLatchy, 2016). In contrast, fore- to hind-limb length ratios did not change with behavior and were very similar between gorilla species despite substantial differences in their habitual substrate use (Ruff et al., 2013). While morphological and behavioral ontogeny were studied conjointly within common chimpanzees (Sarringhaus, 2013b; Sarringhaus and MacLatchy, 2016), because the study grouped morphological data from multiple subspecies, the effects of subspecies

behavioral variation are still unclear. Subtle differences between chimpanzees in behavior may be reflected in skeletal ontogeny, or conversely, it may be that these differences are too small to be detected. Either outcome is important information.

While several studies of phalangeal curvature ontogeny in apes have found that curvature correlates with behavioral change (Paciulli, 1995; Richmond, 2007), again, comparisons have not been carried out at finer taxonomic levels or explicitly contrasted bonobos and common chimpanzees. Finally, most of the studies of morphological ontogeny discussed in previous sections are limited by a lack of chronological age information. To extract the full benefit from ontogenetic analyses, it is useful to consider morphology with respect to behavioral changes in a chronological framework, especially as quantitative ontogenetic behavioral data are presented in this fashion.

Because of this, a complete picture of bonobo morphological ontogeny contextualized within the full range of variation in common chimpanzees is still lacking. The general goals of this study are therefore as follows: 1) to clarify adult morphological differences between *Pan* taxa by determining how and when these differences arise during ontogeny; and 2) to examine relationships between structural properties and reported behavioral variation between taxa, including ontogenetic variation. The following specific hypotheses and predictions will be tested:

Hypothesis 1: Bone length and articular proportions are more phylogenetically or genetically mediated.

1. Bone length and articular proportions will primarily vary among taxa along phylogenetic lines, with greater differences between *P. paniscus* and all *P. troglodytes* subspecies than between any two *P. troglodytes* subspecies.
2. These patterns of taxonomic differences will be apparent and consistent from early in development.

Hypothesis 2: Bone cross-sectional strength ratios and phalangeal curvature are more developmentally and directly behaviorally mediated.

1. Relatively stronger forelimb compared to hind limb and more curved phalanges will be associated with higher amounts of arboreal suspensory and/or climbing behavior both across and within taxa.
2. Within taxa, ontogenetic trajectories for bone strength proportions and phalangeal curvature will parallel ontogenetic change in behavior. In general, the forelimb will become relatively less strong compared to the hind limb with age in all taxa and the phalanges will become less curved.
    a. These changes may take place at different rates in different taxa, in accordance with potential variation in the rate of ontogenetic locomotor transition in different subspecies.
3. Between taxa, bone strength proportions and phalangeal curvature will be most similar among taxa and age groups that share similar behavioral patterns. Variation in ontogenetic trajectories will not necessarily parallel phylogenetic relatedness.
        a. Taxa should be most similar in infancy, when their behavior should be most similar.

4. If adult bonobos resemble immature common chimpanzees in fore- to hind limb strength ratios, this would support the interpretation that they are "locomotor paedomorphs". On the other hand, if adult strength proportions in the two species are similar, this would suggest that locomotor repertoires are also more similar, as suggested by recent behavioral studies.

Hypothesis 3: DMR height is primarily mediated by body size, while DMR angle is more directly a signal of knuckle walking. Metacarpal curvature is also a direct signal of knuckle walking.

1. DMR height will increase with body size both ontogenetically and in adults.
2. Both within taxa during ontogeny and across taxa as adults, steeper DMR angles will be associated with higher frequencies of knuckle walking behavior, where available.
3. Both within taxa during ontogeny and across taxa as adults, metacarpal curvature will track reported frequencies of knuckle walking behavior, where available, with higher curvature associated with more knuckle walking behavior; metatarsal curvature will not, as there is no evidence for a similarly drastic age-related change in foot posture.

2 MATERIALS AND METHODS

This chapter begins by describing the characteristics of the morphological sample used for this study. The protocol for data collection and derivation of additional properties, including both internal and external skeletal measurements and estimation of chronological age from dental development, are then described. This is followed by an explanation of the collation of behavioral data from literature sources to generate the combined behavioral dataset used in analyses. Finally, the methods for statistical data analysis are reviewed.

2.1 SAMPLE

The study sample is comprised of skeletal material from 222 wild-caught *P. paniscus*, *P. t. schweinfurthii, P. t. troglodytes,* and *P. t. verus* individuals, ranging in age from perinatal to adult (Table 2.1). *P. paniscus, P. t. schweinfurthii,* and *P. t. troglodytes* specimens were wild-shot, while *P. t. verus* specimens died natural deaths. Adulthood was defined here as having fully-fused long bone epiphyses and fully erupted mandibular M3's (see below for details on aging of immatures).

Most specimens come from museum collections, including the Smithsonian Institution National Museum of Natural History (NMNH; n = 1 *P. t. schweinfurthii,* n = 9 *P. t. troglodytes*, n = 4 *P. t. verus*), Harvard Museum of Comparative Zoology (MCZ; n = 3 *P. paniscus*, n = 5 *P. t. troglodytes*), Royal Museum of Central Africa (n = 40 *P. paniscus*, n = 44 *P. t. schweinfurthii*), and Powell-Cotton Museum (n = 66 *P. t. troglodytes*). The adult specimens from the Harvard MCZ and the Smithsonian NMNH (n = 22) were included in previous studies (Ruff, 2002). The majority of the *P. t. verus* specimens come from the collections at the Max Planck Institute for Evolutionary

Anthropology at Leipzig (n = 49), which were collected by researchers at the Taï National Park study site, Côte d'Ivoire (Boesch and Boesch-Achermann, 2000). A single additional infant *P. t. schweinfurthii* was obtained from the collections of Adrienne Zihlman at the University of California. Sex was recorded for the majority of the adult sample but was not for the majority of the immature specimens, so sexes are pooled for all non-adults.

All specimens used in the current study were wild-collected, with recorded localities within the known ranges of their subspecies or species. Four adult and four immature individuals originally described as *P. t. troglodytes* had recorded localities within the range of *P. t. ellioti* as currently defined. These individuals did not systematically differ in raw measurements or proportions from *P. t. troglodytes* in their respective age groups. Because of this, and because there is no evidence to date for behavioral differences between these subspecies, these eight individuals are included within *P. t. troglodytes* in the current study.

Table 2.1 Sample

	P. paniscus	***P. t. schweinfurthii***	***P. t. troglodytes***	***P. t. verus***
Young inf (0-2y)	1	2	6	6
Old inf (2-5y)	6	7	9	2
Juvenile (5-10y)	8	12	22	10
Adult Males	15	8	21	12
Adult Females	12	10	22	20
Total*	43	46	80	53

** Because of unknown sex adults, this may be more than sum of other rows*

2.2 MORPHOLOGICAL DATA

All raw measurements collected for this study, including both external measurements and internal bone geometry, are listed in Table 2.2 and Table 2.3. Details of their selection and measurement are discussed below.

2.2.1 External linear measurements

For each individual, measurements of maximum bone length (parallel to the diaphyseal long axis) were taken for the femur, tibia, third metatarsal (MT), humerus, radius, ulna, third metacarpal (MC), and third proximal phalanx. For adults and immature specimens with epiphyses present and fully formed, these lengths were measured using an osteometric board or digital calipers following Ruff (2002). Maximum diaphyseal lengths were measured at all ages until fusion of either or both epiphyses made this measurement impossible, again parallel to the long axis of the bone.

Articular measurements included superioinferior (SI) breadths of femoral and humeral head articular surfaces, ML breadths of distal femoral and humeral articular surfaces and proximal radial and ulnar articular surfaces (using the most distal measurement of the ulnar trochlea as described in the reference below), and AP and ML breadths of MC and MT heads, following criteria laid out in Ruff (2002) and Susman (1979). These measurements were taken on all individuals exhibiting fully formed articular surfaces, but many juvenile specimens lacked epiphyses. For these, diaphyseal lengths and the ML metaphyseal breadths of the distal femur and humerus and proximal tibia, radius, and ulna (at the level of the radial notch) were measured.

In adult specimens, identification of the 3rd metacarpal and metatarsal was based primarily on the morphology of the base and head, as well as the relative lengths and

robusticity of the four other metacarpals or metatarsals. Similar distinguishing features are visible even in very young immature individuals (Baker et al., 2005). Third proximal phalanges were identified by relative lengths and robusticity in both adult and immature individuals, following Susman (1979).

For a small number of *P. t. verus* specimens (six femora and two humeri), physical bones were unavailable for measurement, so corresponding linear measurements were taken on CT scans. To test for measurement bias introduced by this methodological difference, a subset of the sample (all skeletal elements from n=3 individuals) was measured both on CT images and with calipers and an osteometric board. Measurements produced by the two methods were virtually identical (within plus or minus one millimeter).

The right side was used if available, and elements from the fore- and hind limb from the same side were used when possible. Some specimens did not include all elements (especially hands and feet), and while both epiphyseal and metaphyseal breadths were included in the study, availability of these measurements was contingent on developmental stage. Sample sizes for individual analyses are therefore in some cases smaller than the maximum sample sizes indicated in Table 2.1.

Table 2.2 Raw external measurements used in the current study

Variable*	Abbreviation
Lengths	
Femoral maximum/diaphyseal length	FMAXLN/FDIALN
Tibial maximum/diaphyseal length	TMAXLN/TDIALN
Humeral maximum/diaphyseal length	HMAXLN/HDIALN
Radial maximum/diaphyseal length	RMAXLN/RDIALN
Ulnar maximum/diaphyseal length	UMAXLN/UDIALN
3rd Metacarpal max./diaph. length	MCMAXLN/MCDIALN
3rd Metatarsal max./diaph. length	MTMAXLN/MTDIALN
3rd Proximal phalanx max./diaph. length	PMAXLN/PDIALN
Articular dimensions	
Femoral head SI breadth	FHDSI
Distal femoral ML breadth	FDARTML
Proximal tibial ML breadth	TPLML
Humeral head SI breadth	HHDSI
Distal humeral ML breadth	HDARTML
Proximal radial ML breadth	RHDML
Proximal ulnar ML breadth	UPRARTML
3rd Metacarpal AP and ML breadth	MCHDAP/MCHDML
3rd Metatarsal AP and ML breadth	MTHDAP/MTHDML
Metapodial ridges	
3rd Metacarpal dorsal ridge height	MCDMR_H
3rd Metacarpal dorsal ridge angle	MCDMR_A
3rd Metatarsal dorsal ridge height	MTDMR_H
3rd Metatarsal dorsal ridge angle	MTDMR_A
Curvature	
3rd Metacarpal curvature	MC_IA
3rd Metacarpal normalized curvature moment arm**	MC_NCMA
3rd Metatarsal curvature	MT_IA
3rd Metatarsal normalized curvature moment arm**	MT_NCMA
3rd Proximal phalanx curvature	P_IA
3rd Prox. phalanx normalized curvature moment arm**	P_NCMA

** See text for details of measurement of each variable*

*** Standardized by AP section moduli as described in text*

2.2.2 Cross-sectional geometry

2.2.2.1 Images and section locations

True cross sections are more biomechanically informative than external breadths (Ruff, 1987b; Demes and Jungers, 1989; Biknevicius and Ruff, 1992; Jungers et al., 1998), because of variation in the relative size of the medullary cavity and overall distribution of bone within the cross section. For this study, cross-sectional images were obtained using computed tomography (CT) techniques. The majority of the sample was collected using pQCT (peripheral quantitative computed tomography), with a maximum pixel edge length of 0.09 mm (Ferretti et al., 1996) (slice thickness is a constant 1 mm in all scans). This allows for clear visualization of periosteal and endosteal contours even in very young specimens. This pixel size was used for neonates and young individuals, with larger individuals scanned at slightly lower pixel sizes (0.15-0.30 mm in the largest adults). The adult individuals included in previous studies were imaged with medical CT, with a pixel edge length of about 0.30 mm (Ruff, 2002). The *P. t. verus* sample from the Max Planck Institute for Evolutionary Anthropology (MPI) was scanned with micro-CT. For these individuals, adult and near-adult long bones were scanned at 0.091 mm, and immature specimens and hand and foot bones at 0.03 mm.

In addition to the length measurements discussed above, a third (length') was taken on specimens with fused epiphyses and used to identify diaphyseal section locations. Length' is essentially inter-articular length, measured between the centers of the proximal and distal articular surfaces, except for the femur, where the proximal endpoint is the superior surface of the femoral neck (see Ruff, 2002; Marchi, 2005 for details) (Figure 2.1). Cross sections were located at 50% of length' from the distal end of

all bones except the humerus, where cross sections were located at 40% of length' from the distal end (to avoid the deltoid tuberosity). Homologous section locations in immature specimens lacking epiphyses were identified by comparing ratios of length' to ratios of diaphyseal length in specimens exhibiting partial fusion in which both could be measured (see Ruff et al., 2013). In chimpanzees these corresponded to 45% of diaphyseal length from the distal end of the femoral metaphysis, 41% of diaphyseal length from the distal end of the humeral metaphysis, 52% of diaphyseal length from the distal end of the tibial metaphysis, 50% of diaphyseal length from the distal end of the radial and ulnar metaphyses, and 57% of diaphyseal length from the proximal end of the metacarpal and metatarsal metaphyses.

Global positioning of specimens was carried out by aligning the long axis of the bone between the centers of the proximal and distal articular surfaces (or femoral neck, for the femur) as described previously and illustrated in Figure 2.1 (Ruff, 2002; Marchi, 2005). In specimens without epiphyses, bones were aligned using the AP and ML centers of the proximal and distal metaphysis in place of the points of reference used for adult bone. For the majority of the sample, bones were aligned manually prior to locating cross sections. In the *P. t. verus* sample from the Max Planck Institute, three-dimensional renderings from the micro-CT volume were aligned in Avizo software (V7) along the same axes used for physical orientation. Error studies for each skeletal element (n = 5 for each) were performed by re-measuring each five times. These produced values for geometric properties within 1-2% of each other, suggesting that the digital alignments were repeatable.

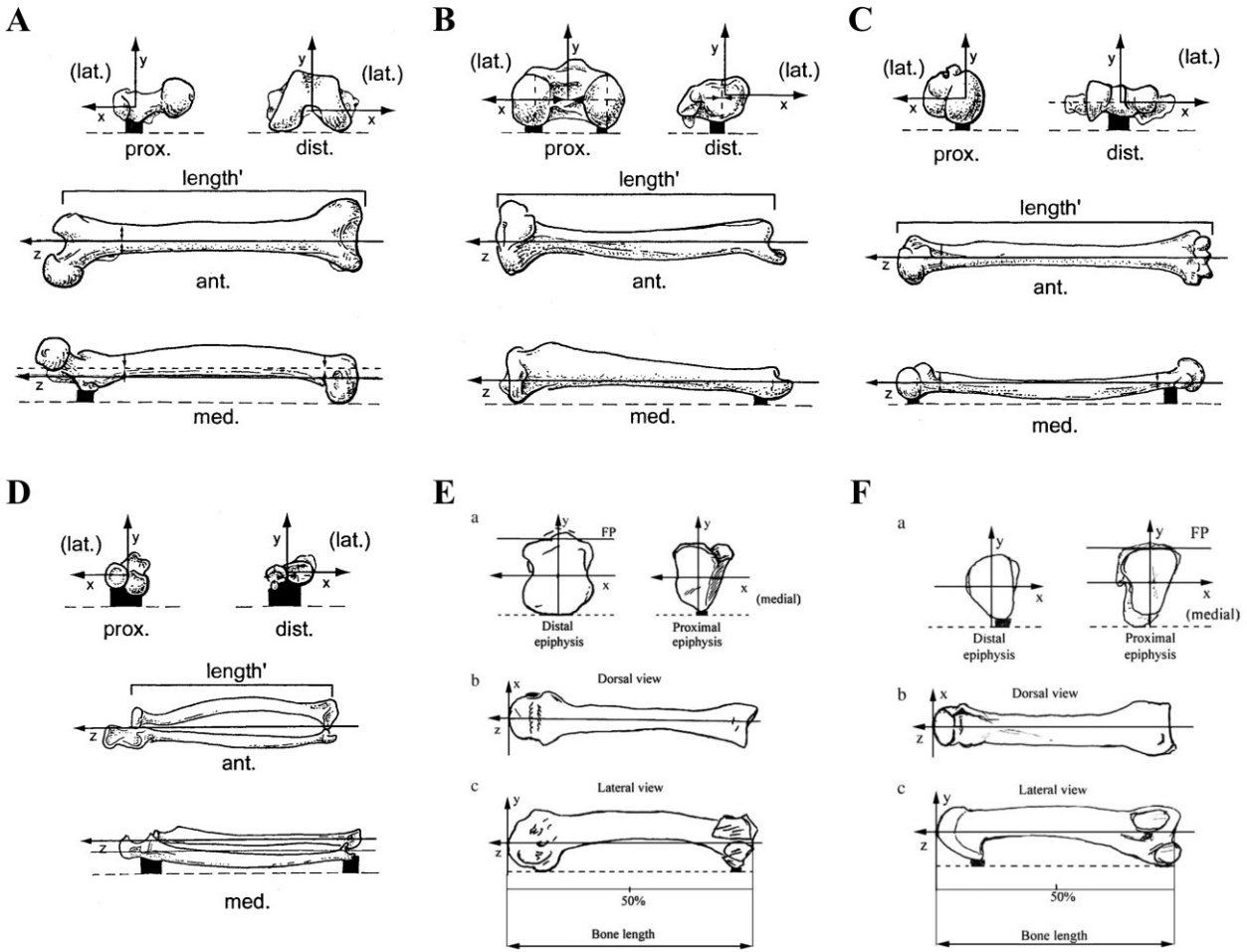

Figure 2.1 Global positioning of long bones for collection of diaphyseal cross sections for (A) Femur, (B) Tibia, (C) Humerus, (D) Radius and Ulna, (E) 3rd Metacarpal, and (F) 3rd Metatarsal. Figure modified from Ruff (2002) and Marchi (2005).

2.2.2.2 Calculation of geometric properties

Variables used in the present study include the ratio of section moduli measured around the x and y axes (Zx/Zy), which is an index of AP/ML bending strength and cross-sectional shape in each section image (Ruff, 2008b), and polar section modulus (Zp). Polar section modulus is generally used as an indicator of bending and torsional strength, although in sections that depart significantly from circularity (where the maximum breadth is more than 1.5 times the minimum breadth), the beam model for torsion becomes less accurate (Daegling, 2002). The only sections in the current study non-circular enough to regularly meet this assumption are from the tibia, but even in this case, Zp is still a good index of average bending strength in two perpendicular planes (Daegling, 2002).

For all scans taken with pQCT, scanner software was used to calculate section properties using a constant bone-air threshold. Validation studies of these calculated properties using cross-sectional phantoms of bone-equivalent materials (see White et al., 1977) showed errors of less than 1% over a full size range of specimens, including smaller sizes than those included in the current study. For the subset of the sample imaged with medical CT, section properties were calculated from images using SLICE (Nagurka and Hayes, 1980) or a version of NIH Image (1.52moi-b5), as described in Ruff (2002). Because the software used for these calculations did not compute section moduli, in previous analyses (Ruff, 2002) section moduli were estimated by dividing second moments of area by ½ the appropriate diameters, which produces results that are internally consistent but systematically biased relative to true section moduli. To include these data in the present study, linear correction equations for these individuals were

computed based on 66 adult or near-adult individuals for which both approximate and true (from pQCT) values were available. %SEE's were low for all equations (1.6-3.14%), with variation likely resulting from differences in section circularity and regularity (see Ruff et al. (2013) for more detail).

Sections imaged with microCT were analyzed in ImageJ (Rasband, 1997) using a freely available macro for geometric cross-sectional property calculation ("Moment Macro", http://www.hopkinsmedicine.org/FAE/mmacro.htm). To determine the appropriate threshold for these calculations, the same bone-equivalent phantoms of varying sizes (see above) were scanned at 0.091 mm and 0.03 mm resolutions, with their diameters and section properties calculated in Moment Macro and compared to true values. No differences were found between the two resolutions, so results from the 0.091 mm scans were used to establish a range of thresholds that gave results within 1-2% of true values for each size, which were then used to threshold the bone specimens. Because bone is still being deposited in developing individuals and may not be fully mineralized (Currey and Butler, 1975), some immature individuals exhibit extremely porous endosteal cortical bone, making it difficult to distinguish the true outline of the endosteal envelope. Following previous studies (Carlson, 2002; Sarringhaus, 2013a) obvious trabecular bone was excluded from scans during this step. This is unlikely to substantially affect the results, as non-cortical bone in mid-diaphyseal regions does not contribute substantially to bone strength or rigidity and its inclusion or exclusion has little impact on estimated values when the cancellous bone makes up less than 40% of the total cross-sectional area (Ruff, 1983).

Table 2.3 Measurements of cross-sectional geometry used in the current study

Variable*	**Abbreviation**	**Description**
Section modulus around ML axis	[*]Zx	Bending strength in the AP plane. Used to calculate Zx/Zy, an index of relative AP/ML bending strength
Section modulus around AP axis	[*]Zy	Bending strength in the ML plane. Used to calculate Zx/Zy, an index of relative AP/ML bending strength
Polar section modulus	[*]Zp	(2x average) bending strength, torsional strength. For some analyses, standardized by body mass*bone length as described in text

** Each variable measured on each bone included. [*] in abbreviation is replaced by letter code referencing specific bone: F = femur, T = tibia, H = humerus, R = radius, U = ulna, MC = 3rd metacarpal, MT = 3rd metatarsal*

2.2.3 Metacarpal, metatarsal, and phalangeal curvature

Longitudinal curvature was measured on the third proximal phalanges and the third metacarpal and metatarsal. There are several different methods available for measuring bone curvature, but for phalanges, the most commonly used is the calculation of included angle (IA; see references below). This method models the neutral axis of a phalanx in side view as conforming to an arc along the circumference of a circle and was initially adopted because it provides a single value of curvature for each phalanx within a species, i.e., it is not length-dependent within taxa (Stern et al., 1995). Because of its broad application and comparatively long history of use, information on phalangeal IA values is available for a broad variety of primate (and non-primate) taxa (Jungers et al., 1997; 2002). The most relevant previous studies of phalangeal curvature ontogeny in great apes have also used this method of measurement (Paciulli, 1995; Richmond, 1998).

Some have argued that IA is, however, not the most appropriate method for measuring curvature because it is a non-linear function of bone length (Ohman and Latimer, 1986) and assumes evenly distributed curvature along the bone, which is not true for many primate phalanges, including those of *P. troglodytes* (Deane and Begun, 2010). Other authors have argued that the curvature moment arm (distance from the neutral axis of the diaphysis to the interarticular line) is most biomechanically meaningful for some bones, since it represents the bending moment arm in that plane (given an applied axial load) (Biewener, 1983; Swartz, 1990). Standardizing this measurement by bone length is mathematically reducible to IA (Stern et al., 1995), but standardizing by AP diameter of the bone (related to AP bending strength) presents a true alternative to

other, length-dependent measures of phalangeal curvature (Swartz, 1990). This index is often used in biomechanical analyses because the AP width of the bone should play a role in determining the bone's bending strength in that plane (Godfrey et al., 1997; Llorens et al., 2001). A more precise measure of AP bending strength is the AP section modulus. Based on the flexure formula for bending,

$\text{stress} = \frac{M}{Z}$, where *M* is the bending moment and *Z* is the section modulus. $M = F * d$, where *F* is the applied force and *d* is the perpendicular distance from the neutral axis of the diaphysis (the AP midpoint here) and the interarticular line. Therefore, $\text{stress} = F * \frac{d}{Z}$, and a larger $\frac{d}{Z}$ ratio produces more bending stress in the bone given the same force. Higher values of NCMA indicate bones that would develop more bending stress (i.e., would be relatively weaker) under axial loadings applied to their ends, and vice versa.

For these reasons, both IA and curvature moment arms standardized by AP section moduli are used in the present study. Medial photographs of the third metacarpal, metatarsal, and proximal phalanx were taken with a digital camera from a distance of approximately 80 cm, with a scale bar included. Photographs were imported into ImageJ (Rasband, 1997) for analysis. IA was calculated following previous studies (Richmond, 1998; Jungers et al., 2002). First, after setting the scale of the image, points were placed at the AP centers of the proximal and distal ends and the midpoint of the shaft (Figure 2.2). These points were then used to calculate three lengths: the chord of the arc inscribed by the bone ($\overline{AB}$), and the two legs of the triangle ($\overline{AC}$ and $\overline{BC}$).

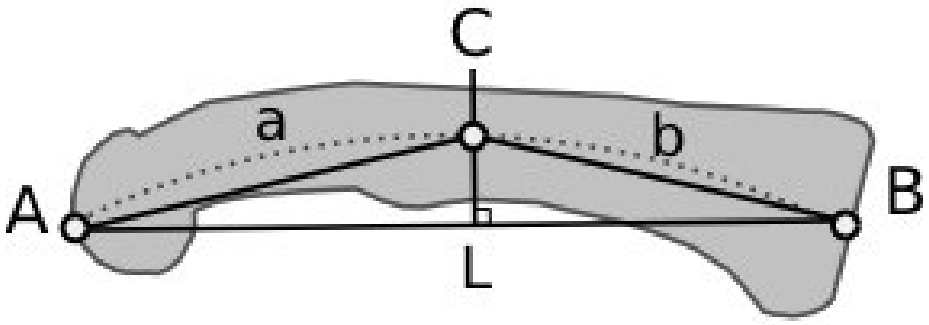

Figure 2.2 Placement of points for calculation of curvature by modeling the phalanx as an arc along the circumference of a circle (grey dashed line). Points A, B, and C, placed at the centers of the proximal and distal articular surfaces and midshaft diaphysis respectively, are used to calculate radius of curvature (RC) and included angle (IA) as described in the text.

The radius of curvature (RC) of the circle can then be calculated with the following equation:

$$RC = \frac{a * b * L}{4 * \sqrt{s * (s - a) * (s - b) * (s - L)}}$$

where $s = 0.5 * (a + b + L)$

Included Angle (IA) is then calculated from RC in the following manner:

$$IA = 2 * \arcsin(\frac{L}{2RC})$$

Corresponding measurements using the midpoints of the proximal and distal metaphyses were taken for individuals lacking epiphyses.

Comparison of curvature measurements in ontogenetic series requires correction for the contribution of the epiphyses to total curvature, since these may be unfused and are often absent in the youngest individuals. If present, unfused epiphyses were manually positioned with clay, and both “diaphyseal” and “maximum” curvature was measured. Following Richmond (1998), the relationship between the two was used to construct

conversion equations from least squares regression of maximum curvature on diaphyseal curvature for the metacarpal, metatarsal, and third proximal phalanx. Relationships were well fit by simple linear models, and there was no evidence for species differences in the relationship between diaphyseal and maximum curvature in any of the three bones, so the following pooled *Pan* equations were used to estimate curvature for all, where *x* is IA based on the diaphysis and *y* is IA based on the entire bone, with epiphyses:

Metacarpal: $y = 6.18 + 1.01x; SEE = 2.33; r^2 = 0.68$

Metatarsal: $y = 7.44 + 0.96x; SEE = 2.47; r^2 = 0.80$

Phalanx: $y = 5.47 + 0.93x; SEE = 2.36; r^2 = 0.88$

These equations were used to convert diaphyseal to total curvature. All further analyses use total curvature (actual if known and estimated if not).

In addition to IA, curvature moment arms were calculated as the perpendicular distance between the AP center of the shaft at its longitudinal midpoint and the midpoint of the interarticular line, the distance between point C and line L in Figure 2.2. These were then normalized by dividing by AP section moduli (Zx), as explained above. Cross-sectional properties were measured for the third MC and MT (see section 2.2.2), so this normalized curvature moment arm (NCMA) measurement for these bones is analogous to those used in previous studies of primate bone curvature (see above). However, cross-sectional properties were not measured for phalanges and the presence of prominent flexor ridges on some specimens makes it difficult to measure A-P diameters from photographs, so phalangeal curvature moment arms were also scaled by metacarpal Zx values. These should still reflect the overall loading of the hand, and so provide a reasonable size standardization for phalangeal curvature.

2.2.4 DMR height and angle

The same photographs used for calculation of metacarpal and metatarsal curvature were used to measure dorsal metacarpal and metatarsal ridge (DMR) height and angle. DMR height was measured following Inouye and Shea (2004), as illustrated in Figure 2.3. Using ImageJ (Rasband, 1997), a line was fit tangent to the articular surface of the metacarpal or metatarsal head just distal to the beginning of the ridge (line AB) and a point was placed on the most dorsal point of the on the ridge (point C). If the angle between A, B, and C is less than 180 degrees, the DMR is said to be "present"; angles greater than 180 degrees are indicative of ridge absence. If the DMR was present, its height was calculated as the perpendicular distance from that line to the most dorsal point on the ridge. Following Sarringhaus (2013a), ridge angle data themselves were also retained and analyzed. DMR was measured on all individuals with present and fully formed epiphyses.

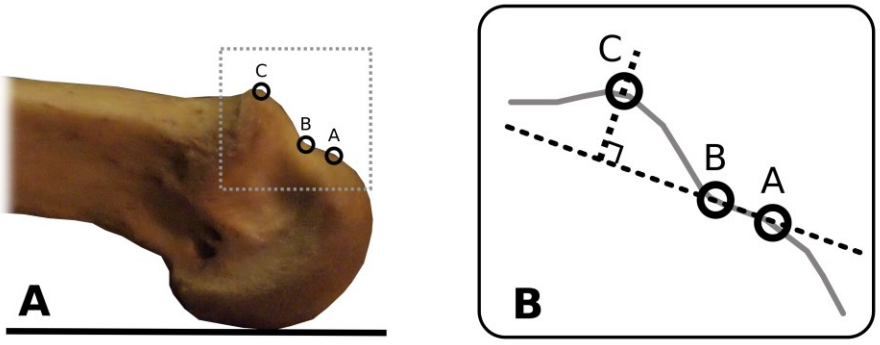

Figure 2.3 Dorsal Metacarpal Ridge (DMR) measurement. (A) Points were placed along the dorsal articular surface as described in the text. (B) DMR presence or absence was determined by ridge angle ($\angle ABC$). DMR was scored as present if less than 180°, and absent if 180° or greater. In addition to ridge angle, DMR height was calculated as the perpendicular length from line $\overline{AB}$ to point C.

2.2.5 Body mass

Because the majority of the sample lacks known body mass, it was necessary to estimate body mass for most of the specimens. There are several existing methods for body mass estimation (including those using both cranial and postcranial variables), each with its own pitfalls and considerations. Caution should be exercised in using postcranial measurements to estimate body mass for use in analyses of other postcranial dimensions, as these variables may functionally covary across taxa. However, while joint dimensions relate to behavior in primates broadly (Jungers, 1988; Godfrey et al., 1991; Rafferty and Ruff, 1994), they are not particularly sensitive to differences in loading during life within taxa (Lieberman et al., 2001). Also, although there are varying degrees of morphological integration between different external bony dimensions in primates (Hallgrímsson et al., 2002; Young, 2006; Young et al., 2010b), estimated body mass is used in this study only to scale cross-sectional properties (which should be primarily mediated by behaviors practiced in life, as discussed previously). Thus, joints and metaphyses were chosen to estimate body mass because they are better body mass estimators than other options such as craniodental measurements and because they can be used to estimate body mass in immature individuals (Ruff et al., 1989; Ruff, 2007).

There have been almost no studies aimed at estimating body mass in juvenile hominoids (but see Hartwig-Scherer and Martin, 1992). This is unfortunate, because the relationship between joint size and body mass may not be constant across ontogeny: in humans, joints tend to "grow ahead" of body mass, so adult equations may overestimate body mass in immature individuals (Ruff et al., 1994; Ruff, 2002; 2003b). Additionally,

younger juveniles have incompletely formed joint surfaces and thus require separate estimates based on metaphyseal breadths. Consequently, individuals with known body mass in the current study were used to devise new body mass estimation equations for both the immature and the adult samples.

Several potential body mass predictors were evaluated based on those suggested by previous studies as potentially informative with respect to body mass (Ruff, 2003b), including SI head breadths of the femur and humerus (FHDSI, HHDSI), distal femoral and humeral ML articular breadths (FDARTML, HDARTML), and proximal tibial plateau ML breadth (TPLML). ML metaphyseal breadths of the distal femur and humerus (FDMETML and HDMETML) were also evaluated for immature specimens. In general, joints were not fully formed enough for measurement of articular breadths until individuals had erupted their second permanent molars, so estimates of body mass from articular dimensions for immature individuals were limited to individuals with erupted M2s. As metaphyseal breadths were measured until fusion of the epiphyses, both metaphyseal and articular breadths were measured on some individuals. Analyses of metaphyseal breadth included all individuals for which it was measured.

For each joint size predictor, body mass estimation equations were generated separately for three reference samples and dimensions: first, articular dimensions in a subset containing only adults (see section 2.3.3 for definition of adulthood); second, articular dimensions in all individuals of M2 dental stage and older (referred to subsequently in this section as the "ontogenetic" sample); and third, metaphyseal breadths for all individuals with the measurement in question. Thus, sample sizes vary for each reference group, and always smaller than the total number of individuals with

known body mass in the study. Each equation was evaluated using the percent standard error of the estimate (%SEE) as a measure of predictive precision, and mean percent prediction error (%PE) as a measure of predictive accuracy (calculated as [(actual-predicted)/predicted]*100, see Ruff (2003b)). Because by definition no adults are included in metaphyseal breadth equations, in order to compare the accuracy and precision of articular and metaphyseal breadths for body mass estimation in older juveniles (where both measurements are sometimes possible), %PE for articular breadths was also calculated separately for all immature specimens from the ontogenetic reference sample equations. Predictors were natural log-transformed, requiring estimated body masses to be transformed back into the original units (kg). This process creates systematic bias, which was corrected for by multiplying by the "quasimaximum likelihood estimator" (QMLE) (Smith, 1993) following Ruff (2003b).

In total, there are 16 known-mass *P. troglodytes* and 12 known-mass *P. paniscus* individuals in the current study, including 15 adult and 13 immature (conservatively, individuals were not included if their body masses were clearly estimated rather than directly measured or if associated museum records indicated that organs or skin had been removed prior to weight measurement). Sample sizes were not large enough for statistical testing of differences between subgroups, but visual inspection of the data did not reveal substantial differences in scaling of joint size to body size between species or subspecies, so they were pooled for all further analyses.

Equations with the lowest %PE's and %SEE's were used to estimate body masses (see below) and are presented in Table 2.4. For adults, femoral and humeral head supero-inferior diameters were among the best body mass estimators. For the ontogenetic

sample, humeral head SI diameter and tibial plateau ML breadth were the best estimators, with %PE and %SEE comparable to those for the best estimators in adults. Equations for the adult-only reference sample always had smaller %PE and %SEE's than their counterparts based on the broader-aged ontogenetic reference sample.

While sample sizes within *Pan* are adequate for articular surface predictors ($n \geq 15$), an insufficient number of individuals with measurable metaphyseal breadths were available to generate estimations even at the genus level ($n = 4$). Metaphyseal breadth scaling patterns were therefore compared to those in *Gorilla* ($n = 26$ individuals with measurable metaphyses and known body masses, obtained from another study (Ruff et al., 2016)) to evaluate whether the two could be combined into a single reference sample. The %SEE's and %PE's for the combined sample are somewhat higher than those for the adult and ontogenetic *Pan*-only articular equations, but are still reasonable when compared to body mass estimation equations from other similar studies (%PE's under 20%; Table 2.4). The distal humerus has slightly higher errors likely because chimpanzees appear to have a relatively smaller distal humerus than gorillas at similar sizes (Burgess et al., 2018).

Femoral head supero-inferior diameter was used to estimate body mass for most of the adults. For adults missing femoral head dimensions ($n = 3$), body mass was estimated from humeral head supero-inferior diameter. For immature specimens with both metaphyseal and articular measurements available, body mass could either be estimated using either an epiphyseal measurement or a metaphyseal breadth. While such dimensions appear to be good body mass estimators for immatures as a whole, it can be difficult to identify the point at which these surfaces are sufficiently formed as to be

comparable to the adult state (see Burgess et al., 2018). To reduce concerns about inclusion of individuals with incompletely formed joints, FDMETML was used to estimate body mass for all juveniles with this measurement present. Body masses for immature individuals missing FDMETML were estimated from the ontogenetic reference sample (including older immatures and adults) for TPLML. For the remaining seven individuals, body mass was estimated from the combined African ape equation for HDMETML. Although less preferable for the reasons discussed above, these individuals were missing most other articular measurements, so this method of body mass estimation was chosen over the alternative of leaving them out of analyses requiring body mass.

Table 2.4 Body mass estimation equations used in the current study

Sample	ln(Predictor)	n	R^2	Slope	Int.	%SEE	%PE	QMLE
Pan (Adult)	FHDSI	15	0.82	2.89	-6.26	13.4	9.5	1.008
Pan (Adult)	HHDSI	15	0.82	3.19	-7.79	13.1	10.0	1.008
Pan (Ontogenetic)	TPLML	22	0.81	2.24	-5.28	17.4	12.5*	1.013
African apes	FDMETML	29	0.96	2.56	-6.90	23.8	14.6	1.025
	HDMETML	30	0.93	2.84	-7.99	29.6	18.8	1.035

** %Prediction error calculated for subset of immature individuals only = 11.1%*

2.3 DENTAL AGING

While many of the *P. t. verus* from the current study have associated age records (n = 34, nine of which were immatures with associated dental development data), the majority of the sample is of unknown age. Tooth calcification was used to estimate chronological age for non-adult individuals lacking associated age records. Dental development is correlated with age (Smith et al., 1994), highly heritable, and generally considered to be more resistant to perturbation via environmental effects than other aspects of somatic maturity such as skeletal size or body mass (Lewis and Garn, 1960;

Garn et al., 1965a; b; Murchison et al., 1988; Marzke et al., 1996), so is generally considered a reliable method of chronological age estimation.

2.3.1 Radiographs and scoring

To assess dental development, radiographs of the mandibular permanent and/or deciduous molars on both the left and right sides were taken in lateral view using a handheld Aribex Nomad Dental X-ray system and AFP Digital sensor on all individuals. These radiographs were used to score dental development according to previous standards based on dividing tooth crown and root development into discrete stages (see below). Deciduous premolars and all three mandibular molars were scored if present, but the third molar was not included in analyses as it is much more variable with respect to age and generally does not increase the accuracy and/or precision of age estimates (Smith et al., 1994; Kuykendall, 1996). Following published methods, for stages based on root development, scores were assigned based on the distal root, and borderline cases were assigned to the earlier stage. Each individual was given a score for each tooth, and one score from each position was used to generate age estimates according to the criteria of the aging system used. Right and left sides usually agreed, but in cases of lack of agreement the less advanced score was used.

All individuals were initially scored and assigned ages based on Kuykendall's (1996) combined-sex data on midpoint age of attainment for captive chimpanzees. Following Smith (1991), estimated age for each individual was calculated as the mean of age estimates at each tooth position. Additionally, a second method was devised using Boughner et al.'s (2012) scoring system in which M1 and M2 scores from this system were summed to create a dental maturity score (DMS). In Kuykendall's (1996) original

statistical method, DMS was then regressed on known age to generate equations used for age estimation. In the current study, sample sizes for the *P. t. verus* specimens of known age (n = 9) were not large enough to generate such equations. However, a previous study (Kralick et al., 2017) has investigated differences between wild mountain gorillas and chimpanzees, comparing dental development between known-age Taï Forest *P. t. verus* and a large sample (n = 41) of known-age, wild mountain gorillas *(G. b. beringei*) from the Volcanoes National Park in Rwanda. Wild mountain gorillas and chimpanzees were not found to differ significantly in their relationship between dental maturity and chronological age (based both on visual inspection and ANCOVA of summary dental maturity score on age). This suggests that a pooled sample is appropriate at this time, although additional data may prove that there are subtle differences between these taxa. Additionally, basing age estimates of wild individuals on captive samples runs the risk of biasing those estimates because of potential differences in the rate of dental development in captive animals (the effects of which may not be constant across all ages (Smith et al., 2010; Boughner et al., 2015)). Thus, DMS-based age estimation equations were based on a combined sample of the known-age wild chimpanzees from the current study and wild mountain gorillas from this previous study (Kralick et al. (2017), n = 9 *Pan*; n = 41 *Gorilla.*) See section 2.3.2 for additional discussion of evidence for captive-wild differences in this sample. The standard error of this equation is within 6 months (Figure 2.4A), comparable to the previous studies discussed above. For these analyses, only chimpanzees and gorillas with no associated error in birth or death date were included.

Because of the pace and timing of permanent dental development, young infants (<1 year) are only represented by a few stages and, by extension, estimated ages. Thus,

age discrimination is relatively poor here (flattened left-hand portion of curve in Figure 2.4a). Deciduous dental development, however, begins before birth and proceeds more rapidly, providing finer age discrimination early in life (Liversidge and Molleson, 2004). For the DMS-based aging method, a subset of the known-age sample with available data for deciduous premolars (n = 2 *Pan*, n = 18 *Gorilla*) was used to generate an aging equation based on deciduous dental maturity scores (DMSd). The youngest individual in the sample was 0.01 years, and the age range was capped at 0.9 years because this represents a natural breaking point in the data scatter below which the relationship between age and DMSd is linear (Figure 2.4B), and because individuals older than this are able to be aged using permanent dentition. The standard error of the estimate is less than one month, indicating that DMSd provides much more precise age estimates for young infants.

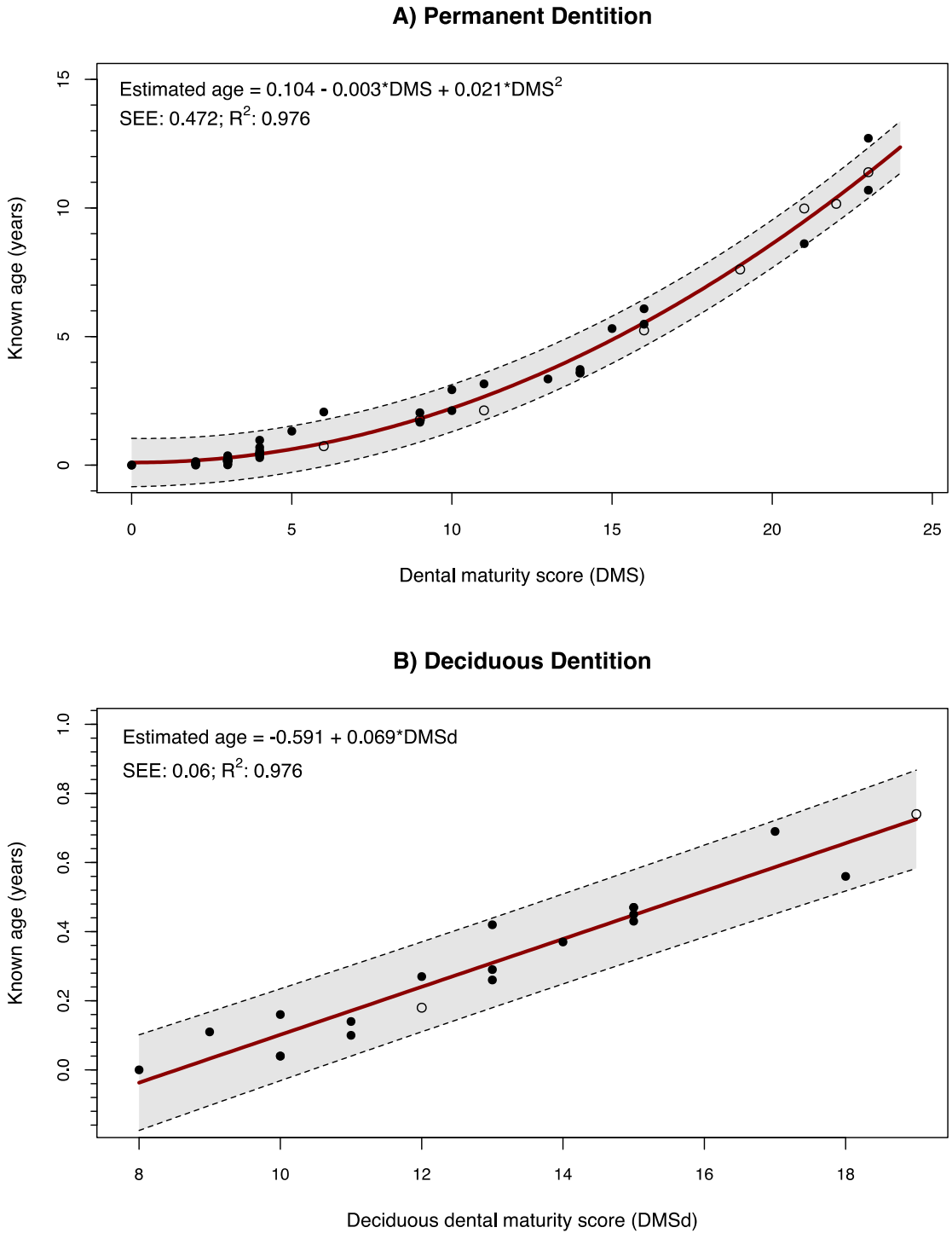

Figure 2.4 Permanent and deciduous dental aging equations. Black points = Gorilla*, open =* Pan*. Regression line and 95% prediction interval are depicted, along with age estimation formulae, correlation, and standard error of the estimate.*

2.3.2 Taxonomic and habitat effects on age estimation

Both of the age estimation methods discussed above are potentially impacted by differences between the reference sample and the current study sample: the first because it is based on captive rather than wild chimpanzees, and the second because it is a based on a combined taxonomic sample of (wild) chimpanzees and gorillas.

The "wild effect" – the prolonging of somatic growth in wild populations compared to their captive conspecifics (Zihlman et al., 2004) – is a potentially serious confounding factor in age estimation. While the magnitude of the wild effect in chimpanzees has been debated (Smith and Boesch, 2011), its existence could bias age estimates in wild animals produced from equations based on captive animals and result in systematic under-aging of wild samples. Unfortunately, there is relatively little data about species or subspecies variation in dental development in *Pan*. Early preliminary information suggested that bonobos may complete their deciduous dentition by as much as six months before common chimpanzees (Smith et al., 1994), although later studies found no differences in deciduous dental formation relative to skeletal maturity between the two taxa (Bolter and Zihlman, 2011; 2012). Evidence from histological studies has suggested that bonobo molars may form slightly more quickly than those of chimpanzee (Ramirez Rossi and Lacruz, 2007), but analyses of the relative timing of tooth mineralization showed no significant differences between the two taxa (Boughner et al., 2012). Combined with their overall similarity in formation time, this has been used to argue for a lack of substantial differences in dental formation rates between common chimpanzees and bonobos (Boughner and Dean, 2008). In general, where the available evidence indicates systematic differences, bonobos have slightly accelerated dental

development relative to chimpanzees, but this seems on the basis of current evidence to be limited to around six months, which is within the margin of error of most age estimation methods, including those employed in this study.

Results from the two different dental age estimation methods are reported along with known chronological age in Table 2.5 for all *P. t. verus* from the aging equation sample that had not completed dental formation of the first and second molars. Because the majority (~95%) of chimpanzees in major research populations in the United States are *P. t. verus* (Ely et al., 2005), differences between known and estimated age using the captive chimpanzee formulae should mostly be due to the wild effect (but see below), while differences between known and estimated age from DMS should mostly reflect the effects of taxon pooling.

Table 2.5 Known and estimated ages for P. t. verus *in age estimation sample.*

ID	Known age	Kuykendall age	DMS age
15015	0.18	0.20	0.29
14993	0.74	0.43	0.86
13432	1.77	1.21	1.81
11777	2.13	2.53	2.66
11788	3.76	4.60*	3.95*
14995	5.24	4.20	5.54
13433	7.60	5.54	7.77
15020	9.98	6.49	9.48
15021	10.16	9.21	10.40
13437	11.39	9.21	11.36

** Age calculated from M2 score for Kuykendall estimate and from mean estimated age of all individuals in the same M2 stage for DMS estimate*

While estimated ages are similar to known ages early in life in both samples, older individuals (after about age 5) are increasingly under-estimated by the captive

chimpanzee standards. This is consistent with previous work (Smith et al., 2010; Boughner et al., 2015) documenting an age effect on the magnitude of captive-wild differences. Ages estimated from DMS equations based on wild populations, in contrast, are more similar to known ages in older individuals (in part because the equations used are based on the same specimens, although this still holds true when these specimens are omitted). Importantly for the purposes of this study, the two estimates are more similar at ages less than five years – the time period when most drastic locomotor changes are taking place. Samples of young chimpanzees are not large enough to directly compare ages estimated from the deciduous dentition equation, but these are also much more similar to known ages for gorillas (not shown) than those estimated from permanent dentition, which tend to be biased upwards for younger and downwards for older individuals.

The fact that the combined wild chimpanzee-gorilla equation performed better than captive chimpanzee-based methods perhaps suggests that the "wild effect" may be stronger than generic-level differences in dental chronologies between African apes, at least at levels detectable in this type of analysis. If true, this would additionally support the lack of large differences at the species and subspecies level within *Pan*. These comparisons may be impacted, however, by other factors, including (but not limited to) relatively larger teeth in gorillas and the potentially heavier disease burdens in the Taï Forest chimpanzees than other wild populations (Smith and Boesch, 2011; Machanda et al., 2015). However, as this study is primarily concerned with producing the most accurate age estimates rather than exploring taxonomic variation in dental chronology,

the combined chimpanzee-gorilla equations are used to generate final age estimates in the skeletal sample.

2.3.3 Final age assignment

Ages for individuals with both permanent and deciduous dental development were estimated from both equations. If the estimated deciduous-based age was younger than 0.9 years, this was assigned as the individual's final age, otherwise the adult-based age was used. Ages for two chimpanzees with missing teeth were estimated from femoral length. Unlike dental development, the relationship between femoral length and age is very different in gorillas and chimpanzees, so the two could not be combined as a single reference sample. However, sample sizes for known age *P. t. verus* are still too small for a separate regression. Thus, femoral maximum length was regressed against known or dentally estimated age. As would be expected, femoral length is correlated with age, and the relationship is linear, although it is considerably less precise than relationships between dental development and known age (Figure 2.5). In three cases, specimens were missing both left and right molars at a given position. These individuals were instead assigned the mean age estimated for all individuals with complete dentitions exhibiting the same stage for their existing teeth. The maximum age estimate from the adult equation is 12.45 years. Individuals with M3 erupted and completed skeletal epiphyseal fusion were designated "adults", and were given an age of 16, as chimpanzee behavioral "adulthood" is between 15 and 16 years of age (Bard, 1995; Rowe, 1996). For most analyses, older adults with known ages were also capped at this value. The oldest individual without complete skeletal fusion but with an erupted M3 was estimated at 12.45 years, and the youngest (known age) individual with complete skeletal fusion is

15.39 years old. The mean of these values (13.93), rounded up to 14, was assigned to all individuals with emerged M3s but incomplete skeletal fusion.

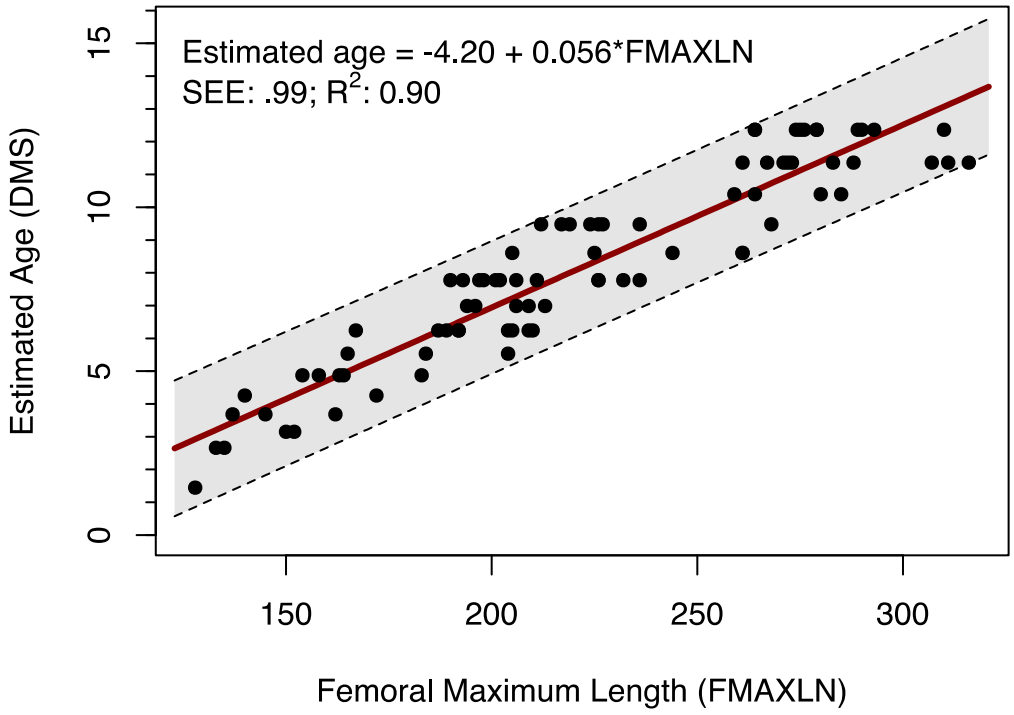

Figure 2.5 Age estimation from femoral maximum length

2.4 BEHAVIORAL DATA

For comparison to morphology, data on locomotor and positional behavior from wild populations of chimpanzees were gathered from the literature, including both adult and ontogenetic data where available (see Table 1.3). With the exception of Taï Forest chimpanzees, the morphological data span a much broader geographic range than these behavioral data, which are studies from single populations. There is likely behavioral variation within each subspecies across these geographic ranges, but because close

correspondence between behavior and morphology at the population level is not possible for the majority of the sample, both behavioral data and morphological data are compared at the subspecies level.

Differences in reported behavioral frequencies between studies may not necessarily represent true population variation because of methodological differences, including sampling protocol, definitions and numbers of behavioral categories, and, for ontogenetic studies, differences in cutoffs of age classes. These factors must be corrected for (as much as possible) prior to comparison between studies.

Sampling protocol was similar across most of the included studies, which used instantaneous focal sampling at either one or two minute intervals. However, behavioral frequencies from Doran (1992b) were calculated from continuous locomotor bout sampling as the proportion of all bouts spent in each activity. Because this method tends to overestimate the frequencies of behaviors occurring primarily over short distances, these data were presented weighted by distance travelled per bout, which should give results similar to instantaneous sampling (Doran, 1989).

The duration and time of year of study may also impact results because of seasonality: for example, *P. t. verus* spend more time on the ground in warm and dry months (Takemoto, 2004). If this is true for chimpanzees in general, the duration and time of year of sampling, as well as the overall degree of seasonality at the site, may impact reported behavioral frequencies. This is difficult to control for, but most of the included studies ran for substantial portions of a calendar year or were on populations living in less seasonal areas, so these effects should be minimal.

In addition to sampling protocol and length of study, variation in definitions of behavioral categories can have a major impact on how comparable studies are to one another. The amount of continuity between any given positional behavioral categories can make the process difficult, and although standardized positional behavioral categories have been introduced that are largely used as the basis for most recent studies (Hunt et al., 1996), studies pre-dating these (including several of those referenced here) often followed slightly different categorizations.

The broadest behavioral categories used in any of the studies of *Pan* are found in Doran (1992b; 1997) and Susman (1980; 1984), each using the same categories. (Although both divided some of these into sub-categories during initial data collection, they are grouped for most analyses). These include quadrupedalism, quadrumanous climbing and scrambling, suspension, leaping and diving, and bipedalism. Hunt (1992) also employs behavioral categories (again, with finer-grained categorizations during data collection aggregated into broader behavioral classes for analysis), but his original categories differ slightly from the above, including quadrupedal knuckle-walking, quadrupedal palm-walking, climbing, bipedal walking, running, brachiating, and "other suspensory locomotion". However, Doran and Hunt later standardized their categories, presenting data in that format for adult *P. t. schweinfurthii* from Gombe and Mahale, adult *P. t. verus* from the Taï Forest, and adult P. *paniscus* from Lomako (for arboreal data only) (Doran and Hunt, 1994). Data for bonobos from Ramos (2014), collected following Hunt's (1992) behavioral categories, are also presented using this same five-category system. The five behavioral categories are defined as follows (all from Doran and Hunt (1994), p 95): *Quadrupedalism*, "a mode of locomotion that employs all four

limbs in a definable gait on a horizontal or a diagonal substrate and includes knuckle-walking, tripedalism, palmigrade quadrupedalism (where hands are not clearly visible), crutch walking, and running"; *Quadrumanous climbing and scrambling*, "a mode of locomotion using hands and feet in varying combinations during unpatterned, diverse gaits that always occur above substrate and include quadrumanous vertical climbing, scrambling, bridging, tree-swaying, and pull-ups"; *Suspensory behavior*, "a positional behavior in which the body's trunk is vertical and suspended below substrate, with the weight borne by forelimbs and includes arm swings, dropping, riding, and crashing foliage to the ground"; *Bipedalism*, "a mode of locomotion in which the body's weight is borne on the hind limbs with the body's trunk vertical and includes bipedalism and aided bipedalism"; *and Leaping and diving*, "a mode of locomotion that includes leaping, diving, and hopping."

However, behavioral data collected by Sarringhaus (2013) are categorized slightly differently because the data collection protocol was designed to explicitly separate behaviors according to their loading of the fore- and hind limbs. The main modes considered in this study are *Bipedal, Bridge, Drop, Forelimb-hindlimb suspensory, Leap, Quadrupedal run, Quadrupedal walk, Ride and sway, Torso-orthograde suspensory, Vertical climb, Vertical descent,* and *Wrestle and somersault* (all based on Hunt et al., 1996), each with several sub-modes. (Although statistical analyses in Sarringhaus (2013) use these broader categories, frequencies are also reported for the sub-modes that make up each category, unlike previous studies). While useful for biomechanical analysis, this makes this study more difficult to compare directly to previous work.

Studies are also not always consistent in compilation of total behavioral frequencies. For most of the above studies, frequencies were pooled by population and compiled directly from raw population-level data. However, Sarringhaus (2013) sampled each individual for the same amount of time and pooled all observations by subject, such that each individual represented a single data point for analysis. Both the equal sampling durations and the pooling of observations reduce the sensitivity of her study to the effects of individual variation and sampling duration compared to those that sample individuals for differing amounts of time and/or do not pool by individual, as without this individuals sampled for relatively more time will contribute more heavily to the overall behavioral profile. This could affect comparisons between the two types of studies, especially in instances of substantial individual variation in behavior. Absent information about the total amount of time for which each individual was sampled for the previous studies, it is difficult to estimate the true effect of this methodological difference.

Lastly, studies of behavioral ontogeny generally pool data into broad age categories and compare behavioral frequencies between these, but methods of categorizing ages and age ranges vary between studies. Sarringhaus (2013) divided her sample into four main age categories based on both behavioral and life history characteristics, with infants and juveniles further subdivided into additional sub-categories (Table 2.6). In contrast, Doran (1992b) defined younger immature age categories by chronological age (with different age cutoffs), but some assignments were based only on behavioral or life history parameters (Table 2.6).

Table 2.6 Age ranges for age bins used in previous and current study

	Sarringhaus		Doran*		This study***	
	Cat.	**Age (y)**	**Cat.**	**Age (y)**	**Cat.**	**Age (y)**
Infancy	Inf 1	0.1 - 2.0	Inf 1	0.0 - 0.5	Young inf.	0.0 - 2.0
	Inf 2	2.1 - 3.0	Inf 2	0.5 - 2.0	Old inf.	2.1 - 5.0
	Inf 3	3.1 - 4.0	Inf 3	2.0 - 5.0**		
	Inf 4	4.1 - 5.0				
Juvenile	Juv 1	5.1 - 7.5	Travels/nests independently, but accompanies mother			5.1 - 10.0
	Juv 2	7.6 - 10.0				
Adolescent		10.1-13	Females immature and nulliparous			10.1 - 14.0
Adult		20.0+	NA			> 14

*P. paniscus *infants not separated into sub-categories*

***Defined as 5 years in Doran (1997), but defined as "independent travel" in the original study*

**** See text for description of age range generation*

In order to compare across populations, data were collapsed with respect to both age and behavior categories. The majority of studies to date (with the exception of Sarringhaus (2013)) have either used or presented their data in accordance with the five main locomotor behavioral categories first used by Doran (Doran, 1989; 1993; Doran and Hunt, 1994). Although these categories are quite broad, because they are available for more samples, data for adult and immature *P. t. schweinfurthii* from Sarringhaus (2013) were collapsed into these. First, the percentages for each behavior were multiplied by the total sampled values to obtain raw count data. These were collapsed into the 5 broad behavioral categories based on descriptions of each behavioral mode from the Appendix and Hunt (Hunt et al., 1996), which were then used to calculate new frequencies of each behavioral mode in each taxon/age class. Because of the need to re-combine certain age classes for comparisons between studies (see below), analyses of ontogenetic change required behavioral frequencies from a subset of age classes within broad age categories. Frequencies of sub-mode for infant *P. t. schweinfurthii* were therefore extracted from

Figure 3 in Sarringhaus et al. (2013). However, in some instances the methods outlined above involved the redistribution of sub-modes within each behavioral mode. Because these sub-modes were only presented in broad age groups in Sarringhaus et al.'s study, for comparisons involving infant *P. t. schweinfurthii*, quadrumanous climbing and scrambling and suspensory behavior were pooled, further reducing the granularity of an already broad categorization.

To generate comparable age categories between studies of *P. t. verus* (Doran, 1989) and *P. t. schweinfurthii* (Sarringhaus et al., 2013), literature data on average age of attainment of behavioral maturity markers were used to assign chronological ages to the ranges of juvenile and adolescent stages for data from Doran (1989). Information on the timing of the life history events used as benchmarks by Doran (1989) suggests that Juvenile covers approximately 5-9y, and Adolescent 9-14y (Bard, 1995). To make age categories directly comparable, Infant 1 and 2 from Doran's studies were collapsed and compared to Sarringhaus's Infant 1, and Sarringhaus's Infant 2-4 were collapsed and compared to Doran Infant 3. These followed a similar procedure to that used to standardize behavioral categories, in which raw count data were aggregated into new age categories and used to calculate frequencies. The final age categories used in the current study are as follows: Young Infant (0-2y), Old Infant (2-5y), Juvenile (5-10y), Adolescent (10-14y), and Adult (14+) (Table 2.6).

While definitions of the older age categories may differ by as much as one year between the two original studies (in the case of the cutoff between Juvenile and Adolescent) and/or involve a degree of uncertainty because of estimated age bins, only eight specimens fall in the period of overlap, so categories were compared directly.

Where available, data on relative frequencies of the five behavioral categories within arboreal contexts is reported in addition to the overall behavioral frequencies. For adults, "arboreality" is calculated as the percentage of locomotor bouts taking place on arboreal substrates.

For *P. t. verus*, all existing data come from a single study, but both *P. paniscus* and *P. t. schweinfurthii* have behavioral data from two or more studies and/or populations. For the current analyses, a "consensus view" of both adult and ontogenetic behavior was therefore calculated for each taxon from the available data (Table 2.7, Table 2.8; results from individual studies are reproduced in Table 6.1 and Table 6.2). Average values for Gombe chimpanzee arboreal behavior are for combined sexes because Doran (1996 Table 16.5) and Doran and Hunt (1994 Table 6) do not present these data separated by sex.

Many studies calculate frequencies of each type of locomotor behavior both as a percentage of total locomotor time and as a percentage of behavior on just arboreal substrates. Studies also commonly calculate "arboreality" defined as the percentage of total time spent on arboreal substrates. Behavioral frequencies relative to total locomotor time are available from at least one study for *P. paniscus, P. t. verus*, and *P. t. schweinfurthii* across all age categories. Arboreality and behavioral frequencies on arboreal substrates are also available for adults from these taxa and for immature *P. t. verus*. However, because these data are not available for immature *P. t. schweinfurthii*, the focus of the ontogenetic portion of this study is on comparing morphological results to frequencies of overall behavior, rather than to arboreality or to frequencies of different

behaviors taking place on only arboreal substrates. Analyses of adults take both types of behavioral information into account.

Because it seems likely that differences between the two populations of bonobos are substantially due to bias from lack of habituation (Ramos 2014), and because the differences themselves are fairly extreme, only the newer data from Ramos (2014) are used here. Unfortunately, this also means that no ontogenetic bonobo behavioral data for bonobos are included; this is considered preferable to including partial ontogenetic data that may be biased.

There are more available published data for *P. t. schweinfurthii* than for any other taxon in the current study. However, within *P. t. schweinfurthii,* it is less clear whether differences between published studies stem from true population differences or from study methods. Because data from the Ngogo chimpanzees (Sarringhaus and MacLatchy, 2016) represent a single ontogenetic trajectory (even if this trajectory is potentially biased relative to other *P. t. schweinfurthii* populations by observer differences), immature and adult data from this population are used for all ontogenetic portions of analyses. Where data for separate sexes is necessary, comparisons use averaged data (within sexes) from Mahale and Gombe (Hunt, 1992), and where possible, information from Ngogo chimpanzees is also used to interpret results. It would be preferable to combine data for all three populations for these comparisons, but as Ngogo chimpanzee adult data are not separated into males and females or presented with information about substrate use, it was decided to use adult data from Mahale and Gombe. This allows retention of information for separate sexes and for arboreality, rather than including this third population in a single average for all adult *P. t. schweinfurthii.* (However, note that

because there were no differences between Mahale and Gombe or between males and females in *arboreal* behavior, these are presented as a single pooled value following Doran and Hunt for inter-subspecies comparisons (1994)).

Lastly, while the "collapsed" behavioral data presented below are used as the initial comparison for morphological data, in some cases (most notably, for hypotheses involving knuckle-walking), additional behavioral data that were not systematically collected or presented across studies, and thus not included in the tables below, may be used to inform interpretations. This will be noted and these data presented in the relevant sections. Locomotor data were not re-tested for statistical significance, but instances where taxa or sexes were found to differ significantly from one another in original studies are noted where appropriate.

*Table 2.7 Adult locomotor frequencies**

		Overall					Arboreal					
Taxon	**Sex**	**Quad**	**C&S**	**Susp**	**Bipedal**	**Leap**	**Quad**	**C&S**	**Susp**	**Bipedal**	**Leap**	**% Arboreal****
P. t. schweinfurthii	M	94.2	4.8	0.6	0.2	0.2	31.1	58.8	6.8	2.6	0.5	33.8
	F	90.8	8.0	0.8	0.4	0.0						52.5
P. t. verus	M	86.6	11.1	1.1	1.2	0.0	11.7	76.7	5.8	5.8	0.0	48.9
	F	85.6	10.9	1.4	1.2	0.6	30.3	59.8	7.4	0.8	1.6	64.8
P. paniscus	M	97.9	1.9	0.1	0.2	0.0	16.0	74.9	2.9	6.3	0.0	41.3
	F	98.1	1.7	0.0	0.1	0.0	20.9	70.8	1.1	5.4	0.0	47.3

** See text for description of each category. Quad = Quadrupedalism, C&S = climbing and suspension, Susp = suspensory. Data for* P.t.schweinfurthii *(Gombe, Mahale),* P. t. verus*, and* P. paniscus *(Lomako) from Doran, 1996, tables 16.3 and 16.5; arboreal data for Mahale* P. t. schweinfurthii *from Doran & Hunt, 1994, table 6; data for* P. paniscus *(Lui Kotale) from Ramos, 2013; data for* P. t. schweinfurthii *(Ngogo) Sarringhaus et al., 2013.*

*** Percent of total observation time spent above the ground*

*Table 2.8 Ontogenetic locomotor frequencies (sexes combined)**

		Overall				
Taxon	**Age**	**Quad**	**C&S**	**Susp**	**CS/Susp****	**Leap**
P. t. schweinfurthii	Young inf	5.9	--	--	87.8	0.0
	Old inf	21.3	--	--	67.2	1.5
	Juv	47.6	30.9	18.8	49.7	0.0
	Adol	66.5	66.5	10.6	32.0	0.7
	Adult	77.5	14.5	6.2	20.7	0.0
P. t. verus	Young inf	10.7	52.9	27.9	80.8	0.7
	Old inf	66.2	23.1	8.6	31.7	1.0
	Juv	92.5	6.3	0.9	7.2	0.0
	Adol	95.1	95.1	0.1	5.5	0.1
	Adult	86.1	11.0	1.2	12.2	0.3

** Data for* P. t. schweinfurthii *from Sarringhaus et al., 2015; Data for P. t. verus and* P.paniscus *from Doran 1989 (Table 6.13, 6.15), 1992*

*** Derived from calculated raw counts of combined climbing and scrambling and suspensory behavior (see text)*

2.5 ANALYSES

The same basic protocol was followed for each skeletal variable analyzed. This section presents a discussion of variables included in the study, followed by an outline of the analyses performed. Further analyses, where warranted, are discussed in the relevant Results sections.

2.5.1 Variables

The raw morphological data collected for this study include absolute bone lengths and joint breadth measurements on limb bones, third metacarpals and metatarsals, and third proximal manual phalanges, as well as measures of cross-sectional strength (Zp) and shape (Zx/Zy) for each of the limb bones and for the metacarpal and metatarsal. Longitudinal curvature of the included hand and foot elements and heights and angles of the dorsal ridges of the third metacarpal and metatarsal were also measured, as described earlier (Table 2.2, Table 2.3).

Hypotheses 1 and 2 center around differences in limb usage and variation in inter-limb loading, which will be tested through analyses of intra- and inter-limb structural proportions. To test hypotheses, these raw measurements must be used to calculate inter- and intra-limb proportions. For these comparisons, nine length, cross-sectional strength, and joint size ratios were calculated: femur/humerus, tibia/radius, tibia/femur, radius/humerus, radius/ulna, metatarsal/metacarpal, metatarsal/tibia, and metacarpal/humerus. Ratios of joint sizes within single bones were also compared, when these were measured (femoral and humeral head/distal femur and humerus, respectively). Because of the large number of individual variables, for simplicity, a tabular summary is

presented at the beginning of each section of the Results chapter listing the specific measurements and ratios analyzed in the section. Additional notes on the selection and calculation of several of these variables are discussed below.

For consistency with previous studies, proportional differences were assessed using logged ratios of structural properties (Ruff, 2003a; b; Ruff et al., 2013; Ruff:2002kn; Sarringhaus and MacLatchy, 2016). Although the proper use of ratios can be complex and is often debated (Smith, 2005), log ratios are appropriate in this instance because in log-log space, variation in log ratios actually reflects deviation from proportional equivalence (see Ruff (2002) for additional discussion).

Because epiphyses are not yet formed in the youngest individuals, in order to examine ontogenetic length trends continuously across the entire age range, from infants through adults, a method for converting between diaphyseal and maximum lengths is necessary. Individuals for which both types of lengths could be measured were used to construct conversion equations from maximum to diaphyseal length for each bone. For better model fits, lengths were log-transformed prior to conversion, and antilogged using a QMLE factor (Smith, 1993). Correlation coefficients were high and percent standard errors of the estimate (%SEE) were low (Table 2.9). Diaphyseal lengths (including the converted lengths) were used in ontogenetic analyses (through adults) and maximum lengths were used for adult-only analyses (see below).

Table 2.9 Equations for estimating diaphyseal length from (natural logged) maximum bone length

Bone (ln)	n	slope	intercept	R^2	%SEE	QMLE
Femur	36	1.01	-0.17	0.99	1.55	1.000121
Tibia	43	0.92	0.30	0.99	1.77	1.000142
Humerus	27	0.97	0.11	0.98	1.40	1.000085
Radius	30	0.94	0.23	0.99	1.18	1.000069
Ulna	13	0.97	0.13	1.00	0.81	1.000032
Metacarpal	31	0.94	0.10	0.98	2.45	1.000293
Metatarsal	30	0.95	0.03	0.94	2.16	1.000897
Phalanx	42	1.01	-0.10	0.99	1.54	1.007639

An alternate means of exploring ontogenetic changes and adult differences in limb bone structural properties is to scale bone strength by the product of body mass and bone length. This acts as a proxy for limb loadings (Selker and Carter, 1989; Polk et al., 2000; Ruff, 2000) and gives an estimate of the strength of the bone relative to predicted loads, which can be informative about life history and behavior and also clarify patterns of change in forelimb and hind limb properties (Young et al., 2010a). Thus, in addition to log ratios of structural properties, scaled cross-sectional strength of each bone individually was analyzed, using body masses and lengths estimated as described in section 2.2.5.

2.5.2 Statistical procedures

All statistical procedures were performed in R with error rate set at .05 (R Core Team, 2014). In cases of multiple statistical tests, it is customary to apply a correction to p values to preserve the overall family-wise error rate. These corrections are appropriate for use when the same test is performed across multiple samples (Perneger, 1998). Therefore, for each skeletal variable in the current study, Bonferroni corections were used when significant differences between age or sex groups were tested between sex or

age categories within the two species or the three *P. troglodytes* subspecies. Prior to each statistical test, all data were checked against the appropriate assumptions (i.e., normality and/or homogeneity of variance). For each variable, analysis proceeded in three phases: first, adult sex and species/subspecies differences were determined, and second, patterns of ontogenetic variation were documented. These were then compared to behavioral data.

2.*5.2.1 Adults*

The analyses described in this section were each performed twice, once comparing *P. paniscus* with *P. troglodytes* as a whole (i.e., all subspecies pooled), and once comparing *P. paniscus* and the three *P. troglodytes* subspecies. Because some differences in levels of sexual dimorphism between taxa in some variables are expected (based on previous studies; see Introduction), each variable was separately tested for differences between males and females within each taxon level analyzed (*P. paniscus* and either pooled *P. troglodytes* or *P. troglodytes* subspecies) using two sample t-tests with unequal variance with Bonferroni-corrected significance levels. 11 individuals of unknown sex were excluded from these calculations. Variables that were not normally distributed were analyzed with Mann-Whitney U tests.

After analysis of sex differences, dimensions were compared between taxa. Most dimensions were normally distributed and were analyzed using t-tests (for comparisons between species) or one-way ANOVA (for comparisons between *P. paniscus* and *P. troglodytes* subspecies). If significant differences between sexes were found, then ANOVAs were performed for males and females separately with a family-wise α of 0.05. Post-hoc tests for subspecies-level analyses were performed with pairwise Games-Howell tests, which work well at small sample sizes and do not assume equal sample sizes or

variances (Games and Howell, 1976). If there were no significant differences between males and females, then sexes were pooled for these analyses and individuals of unknown sex were also included.

Some variables were not normally distributed or violated assumptions of equal population variance (following common protocol, as models are fairly robust to heterogeneity in variance as long as the maximum variance is not more than four times larger than the minimum, this ratio was used to determine the cutoff). Mann-Whitney or Kruskal-Wallis tests were used in these instances, with post-hoc tests for Kruskal-Wallis tests carried out using Games-Howell tests as outlined above. Differences in skeletal proportions were then compared to reported differences in behavioral frequencies.

2.*5.2.2 Ontogenetic*

For this portion of the analyses, adult data were combined into mean male and female values for each variable. First, each variable was tested for a significant relationship with chronological age within each taxon using Spearman correlations, because these do not assume linear relationships. As with adult analyses, correlations were tested both in *P. troglodytes* as a whole and in each subspecies separately. However, these will be poor indicators of more complex (i.e., non-monotonic) changes with age, so more complex models are needed to account for these.

Therefore, to model these relationships and to allow for the examination of differences between taxa over ontogeny, a polynomial regression model was fit to the entire data scatter, with the correct order of the polynomial determined in a forward stepwise fashion until additional terms no longer significantly improved the model at $p < .05$ (following Mays et al., 2009). As with adults, all analyses were performed twice:

once comparing *P. paniscus* to pooled *P. troglodytes*, and once comparing each of the three common chimpanzee subspecies separately to each other and to bonobos. For easier visualization of patterns in complicated data scatters, LOWESS smoothing, a locally weighted polynomial regression (span = .5), was also sometimes used to visualize age-related trends in each taxon separately.

Regression residuals were then used to compare ontogenetic patterns between the taxa. Comparisons between bonobos and the three common chimpanzee subspecies separately used regression residuals from a single pooled regression equation for the genus *Pan*. For comparisons between pooled *P. troglodytes* and *P. paniscus*, an equation was fit to pooled *P. troglodytes*, and residuals were calculated for the bonobos from this equation, with Wilcox rank-sum tests used to test whether these residuals significantly differed from zero (Pinhasi et al., 2005; 2006; Pinhasi, 2008; Mays et al., 2009; Holmes and Ruff, 2011).

As ontogenetic behavioral data are generally reported as pooled frequencies within age cohorts, all analyses of regression residuals were performed within age cohorts matching behavioral literature for comparison (Young Infant (0-2y), Old Infant (2-5y), Juvenile (5-10y), Adolescent (10-14y), and Adult (>14). Residuals from polynomial curve fits were compared between the four taxa within each age cohort using Bonferroni-adjusted pairwise Wilcoxon rank-sum tests (or between two taxa, for species-level analyses). Because only one bonobo fell into the Young Infant age category, these values are presented for visual evaluation but were not statistically analyzed. As with adults, significant morphological differences were then evaluated in the context of the literature behavioral data.

3 RESULTS: LENGTHS, CROSS-SECTIONAL GEOMETRY, AND JOINTS

This chapter is divided into three sections, each one covering a set of related morphological variables: 1) Lengths and Length Ratios, 2) Cross-sectional Geometry, and 3) Joint Sizes and Joint Size Ratios. Each section begins with a table summarizing the variables analyzed, including raw measurements and/or variables derived from raw measurements. This is followed first by analyses of adult sex and species/subspecies differences, then by patterns of ontogenetic variation. Lastly, morphological differences are contextualized with behavioral data.

3.1 LENGTHS AND LENGTH RATIOS

The variables analyzed in this section are found in Table 3.1 and include both absolute and inter-/intra-limb ratios of bone lengths. Ratios were natural log-transformed prior to analyses based on methodological considerations. Raw variables were natural log-transformed for adults for statistical reasons (because some were not normally distributed), but were not for ontogenetic analyses because the statistics employed for these do not assume normality.

3.1.1 Adults

Summary statistics (means and standard deviations) for adult lengths and length ratios can be found in Table 3.2 and Table 3.3.

Table 3.1 Length and length ratio variables

Variable*	Abbreviation
Raw variables	
Femur length	FL
Tibia length	TL
Humerus length	HL
Radius length	RL
Ulna length	UL
3rd metacarpal length	MCL
3rd metatarsal length	MTL
Phalangeal length	PL
Derived variables*	
Femur to humerus length	FHL
Tibia to radius length	TRL
Hindlimb to forelimb length***	HLFL
Tibia to femur length	TFL
Radius to humerus length	RHL
Ulna to radius length	URL
3rd metatarsal to 3rd metacarpal length	MTMCL
3rd metacarpal to humerus length	MCHL
3rd metatarsal to femur length	MTFL
3rd proximal phalanx to 3rd metacarpal length	PMCL

** For ontogenetic analyses, lengths are all diaphyseal, either calculated or measured (see text). These are denoted with lowercase* d *following abbreviation, e.g., "FLd/HLd"*
*** Natural logged for all analyses*
**** Calculated as (FL+TL)/(HL+RL)*

3.1.1.1 Species-level analyses

First, sex differences within *P. paniscus* and *P. troglodytes* were tested with two sample t-tests with unequal variance if variables were normally distributed or Mann-Whitney U tests if not, with Bonferroni-corrected significance levels (family-wide 0.05; Table 3.2). Absolute bone lengths were not significantly different between males and females in *P. paniscus*, but the tibia, radius, ulna, and metatarsal were longer in males than in females in *P. troglodytes*. Previous studies have also found levels of sexual dimorphism in some limb lengths in *P. troglodytes* (Jungers and Susman, 1984). Thus,

conservatively, in inter-species comparisons sexes were analyzed separately for all raw length measurements. No length ratios were found to differ between sexes in either taxon, so the sexes were pooled for analyses of these properties.

Table 3.2 Summary statistics for and sex differences in lengths and length ratios in adults (species)

	P. paniscus						***P. troglodytes***					
	Male			**Female**			**Male**			**Female**		
Variable	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**
FL	9	290.2	10.2	10	292.7	6.3	31	294.5	12.2	42	288.0	16.4
TL	9	245.9	7.6	10	241.6	5.8	31	**248.6**	11.4	43	**241.1**	13.2
HL	9	285.2	10.4	10	288.8	8.2	30	299.1	14.0	42	293.3	16.0
RL	9	266.0	8.6	10	263.3	9.0	30	**274.5**	13.6	42	**265.6**	14.8
UL	9	277.1	10.7	10	277.1	9.6	29	**288.0**	14.5	42	**278.7**	15.3
MCL	7	89.0	3.4	10	86.8	1.4	28	88.8	5.1	37	86.6	5.5
MTL	7	67.8	3.7	10	66.0	1.6	27	**69.9**	4.5	39	**67.6**	4.1
PL	5	51.7	2.7	9	50.2	1.5	23	55.1	3.7	30	55.2	3.1
FHL	9	0.02	0.02	10	0.01	0.03	30	-0.02	0.03	41	-0.02	0.03
HLFL	9	-0.03	0.01	10	-0.03	0.02	29	-0.05	0.03	40	-0.05	0.03
TRL	9	-0.08	0.03	10	-0.09	0.03	30	-0.10	0.03	41	-0.10	0.03
TFL	9	-0.17	0.03	10	-0.19	0.02	31	-0.17	0.03	42	-0.18	0.02
RHL	9	-0.07	0.02	10	-0.09	0.02	29	-0.09	0.03	41	-0.10	0.03
URL	9	0.04	0.02	10	0.05	0.01	29	0.05	0.01	41	0.05	0.01
MTMCL	7	-0.27	0.03	10	-0.28	0.02	27	-0.24	0.03	36	-0.25	0.03
MCHL	7	-1.16	0.06	10	-1.20	0.03	26	-1.21	0.07	36	-1.22	0.06
MTFL	7	-1.45	0.08	10	-1.49	0.04	26	-1.44	0.06	38	-1.45	0.05
PMCL	5	0.56	0.04	9	0.55	0.02	23	0.48	0.04	27	0.46	0.05

Bold values are significantly different between males and females within species
** All variables natural logged for analysis; starred variables non-normally distributed (see text for statistical procedures)*
Bold values are significantly different between males and females within species

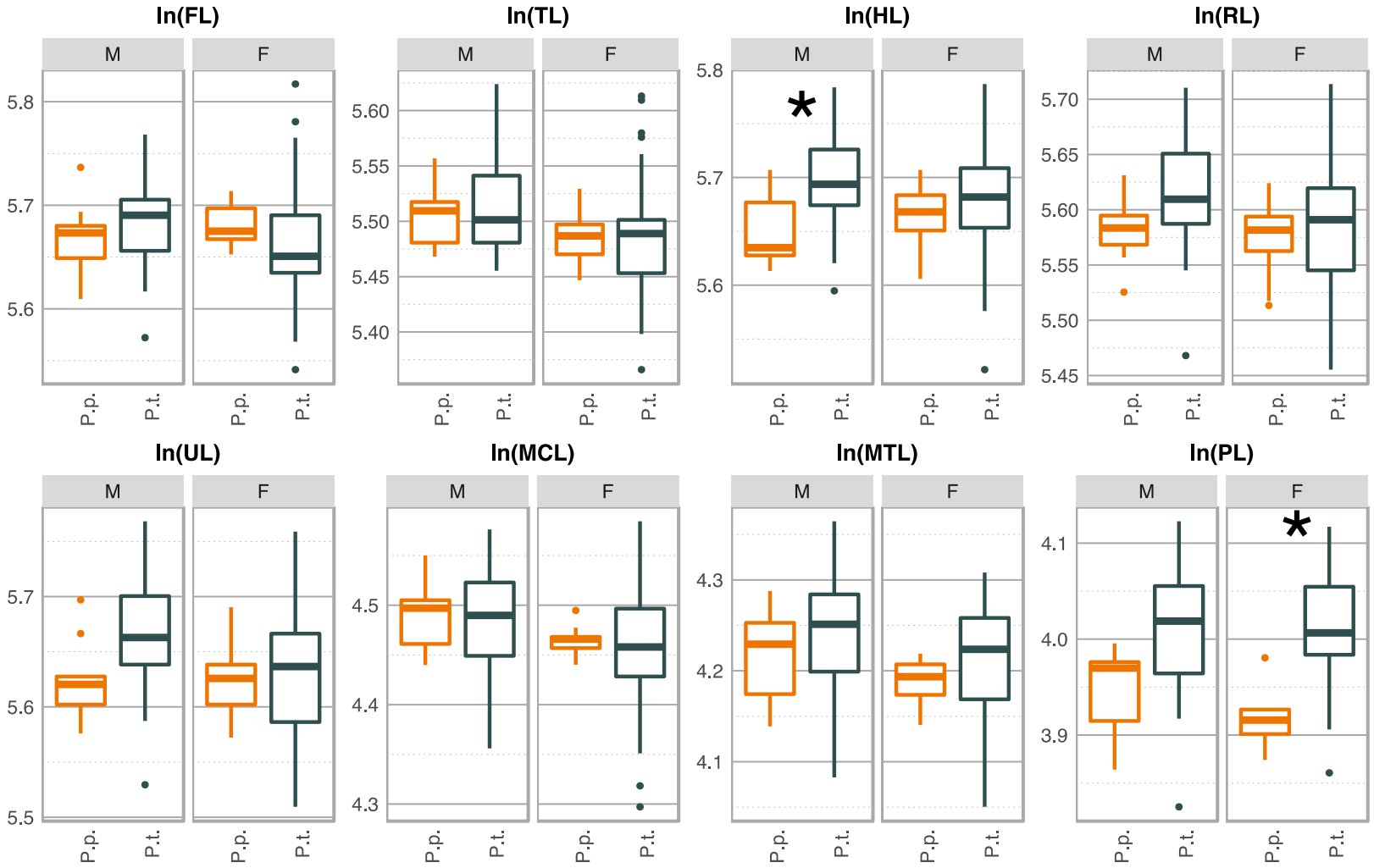

Figure 3.1 Boxplots of maximum bone lengths in P. paniscus *and* P. troglodytes *males and females. Significant differences between taxa (within sexes) are indicated with large black asterisks. P.p.* = Pan paniscus*; P.t.* = P. troglodytes.

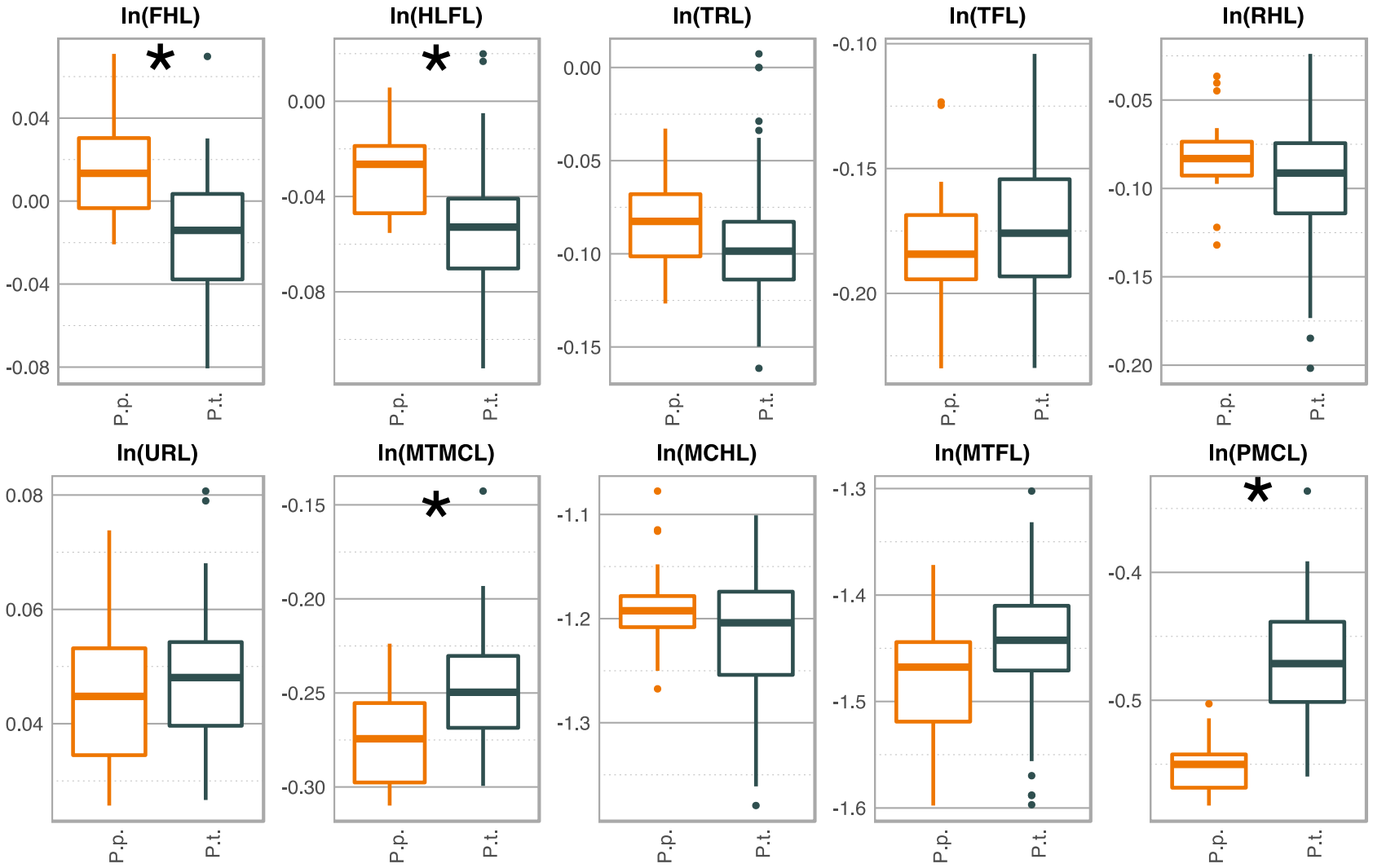

Figure 3.2 Boxplots of bone length ratios in P. paniscus *and* P. troglodytes. *Significant differences between taxa are indicated with asterisks. P.p.* = Pan paniscus*; P.t.* = P. troglodytes.

Figures 3.1 and 3.2 show box and whisker plots for lengths and length ratios respectively, and the results of inter-species comparisons. As with sex differences, species differences were tested with two sample t-tests with unequal variance if variables were normally distributed or Mann-Whitney U tests if not (see Table 3.2). For comparisons of raw properties in males and females separately, significance levels were Bonferroni adjusted ($\alpha < 0.05/2$).

Absolute lengths are significantly different between species only for the humerus (in males) and phalanx (in females), both of which are longer in *P. troglodytes*. In general, the forelimb bones (except for the metacarpal) tend to be less similar between the two taxa than the hindlimb bones, even though significance is not reached.

P. paniscus have a significantly relatively longer femur compared to their humerus and relatively longer total hind limb length compared to forelimb length. The reverse is true for metatarsal to metacarpal and phalanx to metacarpal length, which are significantly higher in *P. troglodytes*. Because metacarpal length is similar between the two taxa (Figure 3.1), the difference in the latter ratio is probably driven by longer phalanges in *P. troglodytes*.

3.1.1.2 Subspecies-level analyses

Sex differences within each subspecies of *P. troglodytes* were investigated using t-tests with unequal variance (for normally distributed variables) or Mann-Whitney U tests (for non-normally distributed variables) at a Bonferroni-adjusted family-wise error rate of .0167 (0.05/3; bonobos were not included in this comparison of sex differences as they were already analyzed in the previous section). No absolute bone lengths or ratios are significantly different between sexes in *P. t. verus* or *P. t. troglodytes*, but the

humerus and ulna are significantly longer in males than in females in *P. t. schweinfurthii* (Table 3.3). The tibia is also significantly longer relative to the femur in males in this taxon. As with species comparisons, because of previous evidence for sexual dimorphism in *P. troglodytes* limb lengths, subspecies differences were analyzed in males and females separately to ensure that pooling of sexes does not bias results (especially given that some sample sizes are small and not balanced between the sexes). All ratios except for tibia to femur length were analyzed with sexes pooled.

Figure 3.3 and Figure 3.4 show box and whisker plots for lengths and length ratios in bonobos and the three common chimpanzee subspecies, as well as significant differences between taxa. Subspecies differences were tested with one-way ANOVA if variables were normally distributed with equal variances, or Kruskal-Wallis tests if not (see Table 3.3). Regardless, all post-hoc tests were carried out with Games-Howell tests at a family-wise error rate of .05. For comparisons in males and females separately, significance levels were Bonferroni adjusted ($\alpha < .05/2$).

ANOVAs show significant differences in raw lengths among the four taxa in the humerus, radius, and ulna in males and in the ulna, metatarsal, and phalanx in females. Of these, *post hoc* tests found that in males, the humerus is significantly longer in both *P. t. schweinfurthii* and *P. t. troglodytes* than in *P. paniscus*, but *P. t. verus* is not significantly different. Both the radius and ulna are significantly longer in male *P. t. troglodytes* than in male *P. paniscus.* (Male *P. t. schweinfurthii* actually has the longest median ulna and radius lengths of any taxa, although they were not found to differ significantly from any others). Male *P. t. verus* also have significantly shorter ulnae than males of the other two *P. troglodytes* subspecies (the only difference between any of the common chimpanzee

subspecies in lengths). Female *P. paniscus* have shorter proximal phalanges than female *P. t. troglodytes* and *P. t. verus*. There is a larger range in phalangeal lengths in female *P. t. schweinfurthii* than in the other taxa, but the median is much closer to bonobo values than to other *P. troglodytes*, and the single phalangeal length available for male *P. t. schweinfurthii* is likewise very short. None of the *post hoc* comparisons were significant in the ulna or metatarsal for females.

There are also significant differences in most of the length ratios, although *post hoc* comparisons do not always reveal significant contrasts between any individual taxa (Figure 3.4). *P.paniscus* have a relatively longer femur compared to their humerus than all three *P. troglodytes* subspecies, and an overall relatively longer hind limb compared to their forelimb than *P. t. verus* and *P. t. troglodytes*. Bonobos also have a relatively longer radius compared to their humerus than *P. t. verus* and a relatively longer metacarpal compared to both their metatarsal and phalanx length than *P. t. schweinfurthii* (although for phalanx/metacarpal length, *P. t. schweinfurthii* are much closer to other *P. troglodytes*, with median values falling well inside the interquartile range of *P. t. troglodytes*). There are also two instances of differences between *P. troglodytes* subspecies: male *P. t. schweinfurthii* have a relatively longer tibia compared to their femur than male *P. t. verus*, and *P. t. troglodytes* have a relatively longer ulna compared to their radius than *P. t. verus.*

*Table 3.3 Summary statistics for and sex differences in lengths and length ratios in adults (*P. troglodytes *subspecies; see Table 3.2 for* P. paniscus)

	P. t. schwein.						***P. t. trog.***						***P. t. verus***					
	Male			**Female**			**Male**			**Female**			**Male**			**Female**		
Variable	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**
FL	3	300.3	15.5	8	281.8	24.3	18	294.2	12.7	19	289.1	15.2	10	293.2	11.1	15	289.9	13.0
TL	3	261.0	15.5	8	235.3	18.2	18	249.6	11.4	19	244.2	12.6	10	243.3	7.2	16	240.4	10.4
HL	3	**309.3**	5.5	8	**281.8**	22.8	18	300.5	14.2	19	295.2	15.5	9	292.9	13.7	15	297.1	9.4
RL	3	282.0	13.2	8	253.0	12.0	18	278.7	11.6	19	268.4	16.4	9	263.7	12.2	15	268.9	10.6
UL	2	**302.5**	4.9	8	**264.5**	12.9	18	292.8	12.1	19	283.2	16.6	9	275.1	11.4	15	280.6	10.2
MCL	2	86.7	12.5	7	83.7	4.1	18	89.6	5.0	19	88.2	6.6	8	87.3	3.4	11	85.6	2.8
MTL	2	69.0	13.6	7	64.2	3.5	18	70.1	4.2	19	68.5	4.7	7	69.7	2.5	13	68.2	2.2
PL	1	45.8	NA	3	52.2	6.3	18	55.7	3.2	18	55.9	2.8	4	54.5	3.4	9	54.7	2.1
FHL	3	-0.03	0.05	8	0.00	0.02	18	-0.02	0.02	19	-0.02	0.03	9	0.00	0.03	14	-0.02	0.03
HLFL	3	-0.05	0.03	8	-0.03	0.03	18	-0.06	0.02	19	-0.06	0.03	8	-0.04	0.03	13	-0.06	0.02
TRL	3	-0.08	0.02	8	-0.07	0.04	18	-0.11	0.02	19	-0.09	0.04	9	-0.08	0.04	14	-0.11	0.02
TFL	3	**-0.14**	0.01	8	**-0.18**	0.02	18	-0.16	0.03	19	-0.17	0.02	10	-0.19	0.04	15	-0.19	0.02
RHL	3	-0.09	0.04	8	-0.11	0.04	18	-0.08	0.02	19	-0.10	0.03	8	-0.11	0.04	14	-0.10	0.02
URL	2	0.04	0.00	8	0.04	0.01	18	0.05	0.01	19	0.05	0.01	9	0.04	0.01	14	0.04	0.01
MTMCL	2	-0.23	0.06	7	-0.27	0.01	18	-0.25	0.02	19	-0.25	0.03	7	-0.22	0.02	10	-0.24	0.03
MCHL	2	-1.27	0.13	7	-1.20	0.05	18	-1.21	0.07	19	-1.21	0.06	6	-1.20	0.07	10	-1.24	0.05
MTFL	2	-1.48	0.13	7	-1.48	0.06	18	-1.43	0.06	19	-1.44	0.05	6	-1.43	0.05	12	-1.45	0.05
PMCL	1	0.53	NA	3	0.47	0.06	18	0.48	0.04	18	0.46	0.05	4	0.47	0.01	6	0.46	0.02

Bold values are significantly different between males and females within subspecies

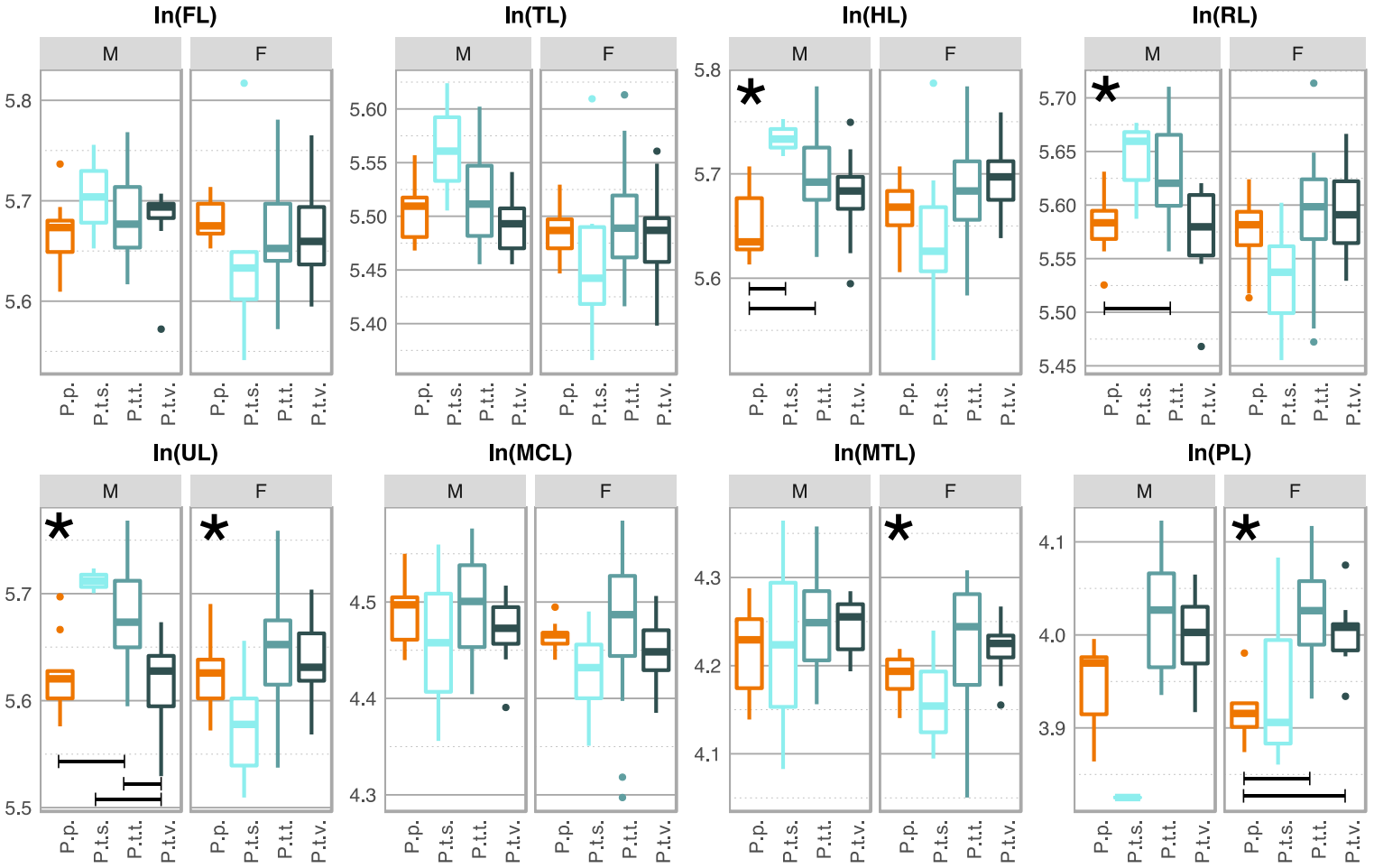

Figure 3.3 Boxplots of bone lengths in P. paniscus *(P.p.),* P. t. schweinfurthii *(P.t.s.),* P. t. troglodytes *(P.t.t.), and* P. t. verus *(P.t.v.). Significant overall differences between taxa (within sexes) are indicated with large black asterisks; significant post-hoc comparisons are indicated with brackets.*

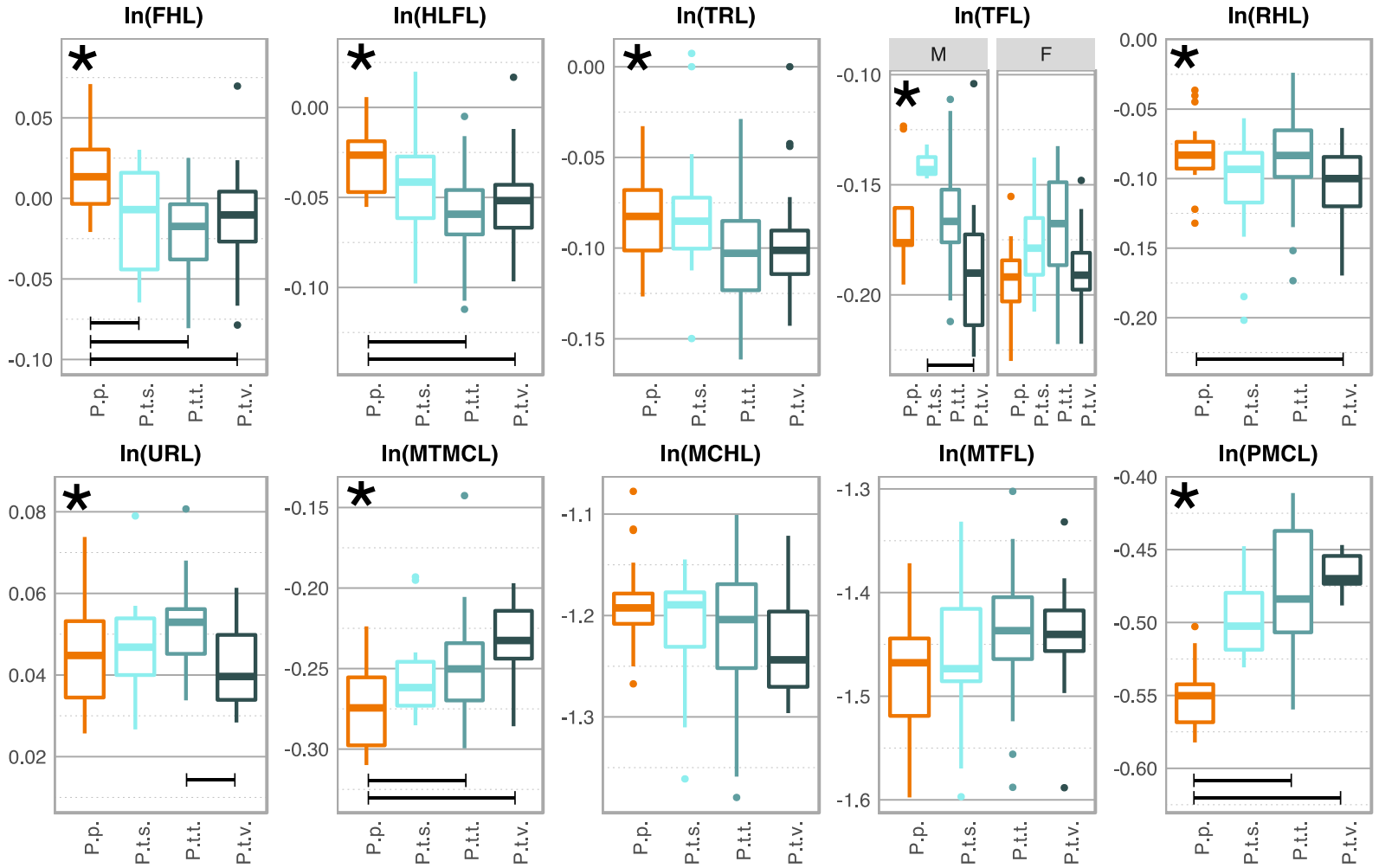

Figure 3.4 Boxplots of bone length ratios in P. paniscus *(P.p.),* P. t. schweinfurthii *(P.t.s.),* P. t. troglodytes *(P.t.t.), and* P. t. verus *(P.t.v.). Significant overall differences between the four are indicated with large black asterisks; significant post-hoc comparisons are indicated with brackets.*

3.1.1.3 Summary

There are a number of length and length ratio differences between bonobos and common chimpanzees. Raw lengths are generally not significantly different between bonobos and pooled *P. troglodytes*, perhaps because (as shown in subspecies comparisons) bonobos are often more similar to one subspecies than they are to the others, although the patterns of similarities and differences are not consistent. Length ratios that differ significantly between *P. paniscus* and *P. troglodytes* also show significant differences with at least one *P. troglodytes* subspecies, with the exception of radius/humerus length, which is longer in *P. paniscus* than *P. t. verus* but not *P. troglodytes* in general. There are also two instances (ulna/radius and tibia/femur length) in which two *P. troglodytes* subspecies differ from each other, both involving *P. t. verus*.

Compared to common chimpanzees as a group, bonobos have a relatively long femur compared to their humerus, which appears to be the result of underlying similarity in femoral length and a shorter humerus in bonobos. Bonobos also have a relatively longer total hind limb length compared to forelimb length than other *Pan*. While *P. paniscus* femoral/humeral length is larger than that of all three common chimpanzee subspecies, total fore/hind limb length is only significantly different between bonobos and *P. t. troglodytes* and *P. t. verus*, not *P. t. schweinfurthii.*

P. paniscus also have a longer metacarpal relative to metatarsal and phalangeal length than both *P. t. troglodytes* and *P. t. verus*. *P. t. schweinfurthii* does not differ significantly but is closer to *P. paniscus* in metatarsal/metacarpal length than in phalangeal/metacarpal length (in which it is much more similar to other *P. troglodytes*).

3.1.2 Ontogenetic

3.1.2.1 Overall correlations with age

Spearman correlations with age in each taxon for all variables are found in Table 3.4. (Note that, as described earlier, for older individuals with fused epiphyses, maximum lengths were converted to diaphyseal lengths, and the means for males and females were used to represent adults.) The direction of change is the same for each ratio across all taxa: not only do lengths increase with age (as expected), but hind limb bones also become relatively longer compared to forelimb bones, and distal limb elements become relatively shorter compared to more proximal limb elements. Hand elements become relatively shorter than limb segments, and the phalanx becomes relatively shorter compared to the metacarpal.

Most, but not all, of these changes reach statistical significance. All raw length measurements are significantly positively correlated with age in all taxa. Hind limb/forelimb length also uniformly increases with age. All other ratio measurements change significantly with age in *P. troglodytes* as a whole, but only metacarpal/humerus, metatarsal/femur, and phalanx/metacarpal lengths are also significant in all subspecies – the others generally show significant change in one or two ratios (possibly because of smaller sample sizes). Length ratios involving hand and foot bones do not change significantly with age in *P. paniscus* (although again, this may be due to sample size). Overall, however, the direction and relative strength of ontogenetic correlations are similar in the two species.

Age-related changes within species and subspecies were examined further using polynomial models of the correct order as determined using forward stepwise selection. Results are presented in the next two sections.

Table 3.4 Correlations and significance for lengths and length ratios with age

	P. paniscus	***P. troglodytes***	***P. t. schwein.***	***P. t. trog.***	***P. t. verus***
Variable	**rho***	**rho**	**rho**	**rho**	**rho**
FLd	**0.94**	**0.96**	**0.96**	**0.95**	**0.97**
HLd	**0.93**	**0.96**	**0.95**	**0.96**	**0.97**
TLd	**0.94**	**0.96**	**0.94**	**0.95**	**0.96**
RLd	**0.94**	**0.96**	**0.95**	**0.95**	**0.98**
Uld	**0.95**	**0.96**	**0.95**	**0.96**	**0.97**
MCLd	**0.88**	**0.95**	**0.92**	**0.94**	**0.97**
MTLd	**0.88**	**0.95**	**0.90**	**0.95**	**0.97**
PLd	**0.82**	**0.95**	**0.94**	**0.94**	**0.96**
FHLd	**0.68**	**0.34**	**0.46**	0.22	**0.48**
HLFLd	**0.95**	**0.96**	**0.95**	**0.95**	**0.97**
TRLd	**0.56**	**0.21**	**0.40**	0.11	0.05
TFLd	**-0.52**	**-0.49**	-0.35	**-0.50**	**-0.61**
RHLd	**-0.43**	**-0.34**	-0.26	**-0.41**	-0.39
URLd	**0.55**	**0.31**	0.36	0.26	0.22
MTMCLd	0.38	**0.34**	0.26	**0.49**	0.04
MCHLd	-0.31	**-0.58**	**-0.56**	**-0.57**	**-0.65**
MTFLd	-0.36	**-0.55**	**-0.55**	**-0.51**	**-0.57**
PMCLd	-0.38	**-0.46**	**-0.63**	**-0.39**	**-0.68**

** bolded values are significant at $p < .05$*

3.1.2.2 Species-level analyses

Species-level differences were examined by calculating bonobo residuals from a polynomial fit to the pooled chimpanzee sample, with Wilcox rank-sum tests used to test whether these residuals significantly differed from zero in all age/taxon groups with sufficient sample sizes. Adult differences were tested in the previous section, so subsequent discussion in this section is in reference to the non-adult age cohorts only.

Table 3.5 contains species means and standard deviations in each age group, along with statistical significance of differences between species from residual analyses.

Overall, bonobos and common chimpanzees appear to follow similar patterns in trajectories of diaphyseal lengths, with more rapid increases early in life and a plateau at around age 13 (see Figure 3.5 for example). Bonobo data are sparse for both very young and adolescent individuals. Growth trajectories for absolute diaphyseal lengths are fit best with fourth or fifth order polynomials, except for metacarpal and metatarsal lengths, which are fit best by third order polynomials, and phalangeal lengths, which are fit best with a first order model (see next section for equations). Bonobos are not significantly different from common chimpanzees in any age cohort for any absolute diaphyseal lengths.

Ratios are more variable in their ontogenetic trajectories. Those involving more proximal limb bones are best fit by simple first order polynomials, while those involving the metacarpal and metatarsal are best fit by third order polynomials (see Figure 3.6, next section). Bonobos and common chimpanzees are similar in tibia/femur length, which gradually decreases with age, and in metatarsal/femur and metacarpal/humerus lengths, which decrease more rapidly early in life and plateau sometime in the juvenile period (Figure 3.6). There are no statistically significant differences between the two taxa in any of these relationships (Table 3.5). However, the two taxa are different in femur/humerus and ulna/radius length. In the former, the two start out more similar, and while relative femur length increases in both taxa, this is much more drastic in bonobos than in common chimpanzees, reaching statistical significance in juveniles and adolescents (Table 3.5 and see Figure 3.6). Bonobos also have a relatively short ulna compared to their radius at all

ages, although again, this only reaches statistical significance in juveniles and adolescents (Table 3.5 and see Figure 3.6).

Table 3.5 Mean and (SD) of variables within each species/age group

	Young Inf. (0-2y)				Old Inf. (2-5y)			
	P. pan.		***P. trog.***		***P. pan.***		***P. trog.***	
Variable	*n*	*mean(SD)*	*n*	*mean(SD)*	*n*	*mean(SD)*	*n*	*mean(SD)*
FLd	1	102.00 (NA)	14	94.04 (19.57)	5	132.37 (8.02)	18	138.28 (15.34)
HLd	1	105.00 (NA)	14	97.69 (20.12)	6	138.87 (8.49)	18	146.73 (15.58)
TLd	1	86.00 (NA)	14	81.51 (16.20)	6	113.37 (7.24)	18	116.74 (11.74)
RLd	1	102.00 (NA)	14	92.79 (19.16)	6	132.11 (9.02)	18	135.96 (13.43)
Uld	1	105.00 (NA)	13	99.35 (22.46)	6	139.91 (9.32)	18	146.50 (14.91)
MCLd	1	34.28 (NA)	13	31.09 (5.92)	5	39.20 (0.80)	16	42.06 (3.99)
MTLd	1	25.64 (NA)	12	25.33 (2.53)	5	29.72 (2.05)	15	31.74 (2.99)
PLd	1	24.65 (NA)	13	24.34 (4.35)	3	29.46 (2.95)	14	31.85 (3.27)
FHLd	1	-0.029 (NA)	14	-0.038 (0.015)	5	-0.043 (0.011)	18	-0.060 (0.025)
HLFLd	1	5.322 (NA)	14	5.212 (0.229)	5	5.578 (0.067)	18	5.612 (0.104)
TRLd	1	-0.171 (NA)	14	-0.128 (0.021)	6	-0.153 (0.029)	18	-0.153 (0.017)
TFLd	1	-0.171 (NA)	14	-0.141 (0.021)	5	-0.158 (0.016)	18	-0.168 (0.028)
RHLd	1	-0.029 (NA)	14	-0.051 (0.019)	6	-0.050 (0.031)	18	-0.075 (0.032)
URLd	1	0.029 (NA)	13	0.070 (0.024)	6	0.058 (0.011)	18	0.074 (0.012)
MTMCLd	1	-0.290 (NA)	11	-0.263 (0.038)	5	-0.279 (0.053)	15	-0.275 (0.033)
MCHLd	1	-1.119 (NA)	13	-1.145 (0.064)	5	-1.252 (0.048)	16	-1.232 (0.058)
MTFLd	1	-1.381 (NA)	12	-1.367 (0.071)	4	-1.494 (0.019)	15	-1.446 (0.074)
PMCLd	1	-0.330 (NA)	13	-0.242 (0.029)	3	-0.286 (0.103)	14	-0.289 (0.051)
	Juv. (5-10y)				**Adol. (10-14y)**			
FLd	8	186.99 (23.07)	41	190.41 (18.85)	8	250.95 (17.04)	20	256.27 (15.72)
HLd	8	189.41 (22.97)	43	197.83 (17.26)	8	250.04 (16.95)	20	261.28 (15.46)
TLd	8	153.17 (19.36)	39	158.12 (15.88)	7	208.63 (13.99)	18	212.11 (11.22)
RLd	8	173.29 (19.51)	43	182.37 (16.55)	8	230.34 (14.39)	19	236.84 (15.40)
Uld	8	184.73 (20.16)	42	198.18 (18.69)	8	246.79 (16.68)	19	259.98 (14.99)
MCLd	6	53.80 (6.02)	39	55.56 (6.44)	8	71.63 (5.46)	19	71.20 (4.95)
MTLd	6	40.54 (5.83)	35	42.79 (4.97)	8	55.64 (3.92)	18	56.66 (4.48)
PLd	4	36.60 (5.14)	31	41.10 (3.93)	7	49.97 (5.48)	12	51.89 (4.18)
FHLd	8	**-0.013 (0.021)**	41	**-0.041 (0.029)**	8	**0.004 (0.016)**	20	**-0.019 (0.017)**
HLFLd	8	5.884 (0.110)	39	5.920 (0.095)	7	6.181 (0.066)	18	6.208 (0.052)
TRLd	8	-0.125 (0.025)	39	-0.147 (0.030)	7	-0.103 (0.016)	18	-0.117 (0.029)
TFLd	8	-0.200 (0.014)	39	-0.185 (0.033)	7	-0.191 (0.028)	18	-0.195 (0.029)
RHLd	8	-0.088 (0.030)	43	-0.082 (0.032)	8	-0.082 (0.017)	19	-0.097 (0.034)
URLd	8	**0.064 (0.010)**	42	**0.080 (0.012)**	8	**0.069 (0.008)**	18	**0.085 (0.007)**
MTMCLd	6	-0.286 (0.030)	35	-0.271 (0.036)	8	-0.252 (0.021)	18	-0.232 (0.029)
MCHLd	6	-1.265 (0.039)	39	-1.268 (0.057)	8	-1.251 (0.041)	19	-1.299 (0.055)
MTFLd	6	-1.530 (0.042)	35	-1.491 (0.055)	8	-1.507 (0.044)	18	-1.510 (0.066)
PMCLd	4	-0.410 (0.018)	31	-0.293 (0.052)	7	-0.366 (0.069)	12	-0.326 (0.053)

Bold values significantly different between species at family-wise alpha of .05

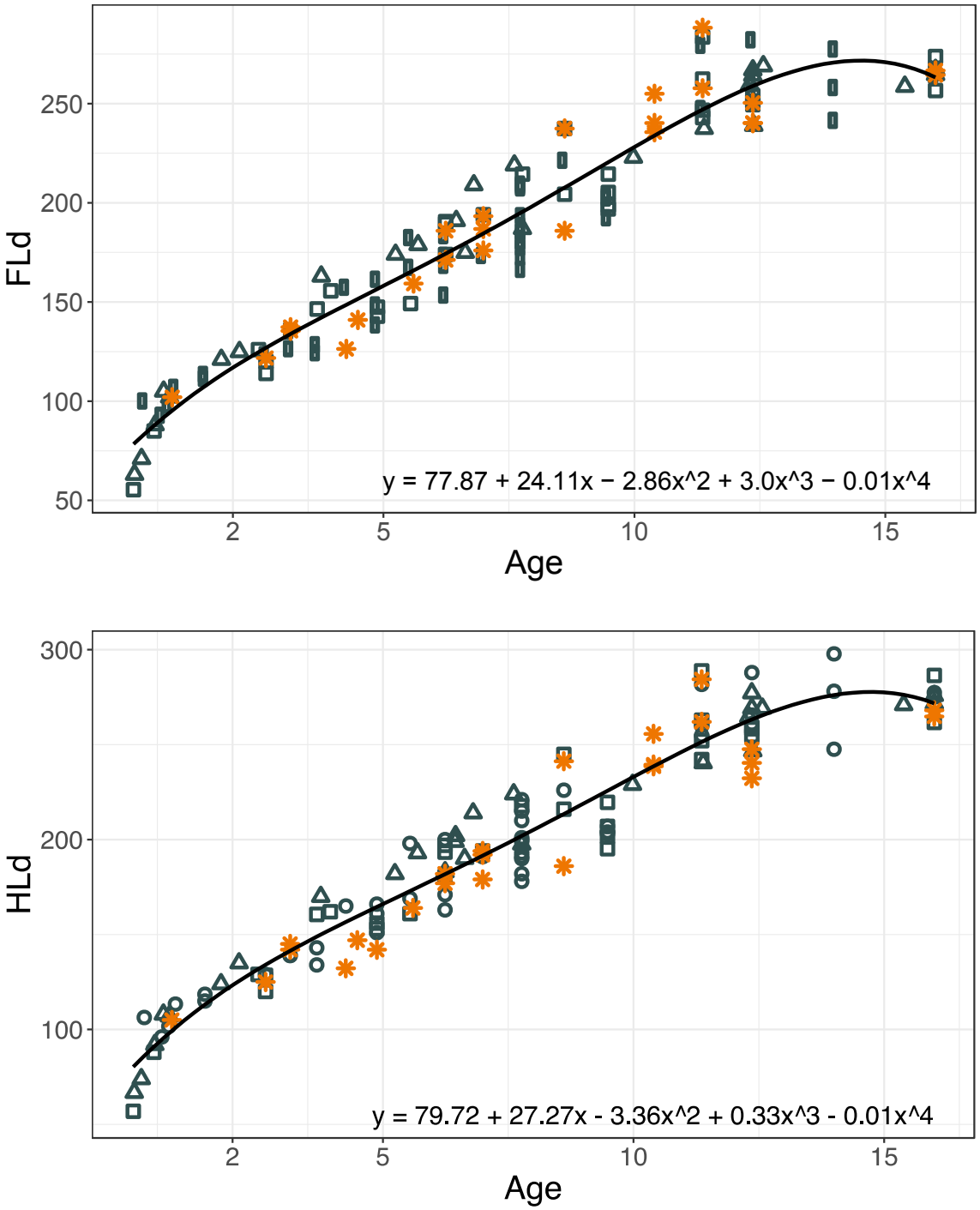

Figure 3.5 Examples of growth in diaphyseal length. P. paniscus = *orange,* P. troglodytes = *blue (*P. t. schweinfurthii = *squares,* P. t. troglodytes = *circles,* P. t. verus = *triangles). Black line is the pooled total sample equation*

3.1.2.3 Subspecies-level analyses

Subspecies-level differences were examined visually using LOWESS fits and statistically using residuals for each subspecies (and bonobos) from a pooled line fit to the entire data scatter. Bonferroni adjusted pairwise Wilcox rank-sum tests were used to test whether these residuals significantly differed between taxa within any of the groups (except for Young Infants, because of inadequate sample size; see Methods). As with species-level analyses, adult differences were tested in the previous section; this section is in reference to the non-adult ages only. The variables that were tested for differences between species in the previous section are retested here at the subspecies level.

Plots of diaphyseal length ratios against age are shown in Figure 3.6. Boxplots for values of selected ratio residuals in each age group are shown in Figure 3.7, with complete summary statistics for each variable found in the Appendix. Again, fourth order polynomials are the best fits for limb bone length growth, and third order polynomials are the best fit for metacarpals and metatarsals, with first order polynomials for phalanges (see previous section). As with species-level differences, diaphyseal lengths are similar across the four taxa in all age cohorts. The one exception to this is humeral diaphyseal length (Figure 3.5), which is transiently significantly higher in *P.t .verus* than in *P. t. troglodytes* in the juvenile age class (Table 3.6; Figure 3.5).

First and third order polynomials are the best fits for change in length ratios with age. In addition to the polynomial fit to the pooled sample, each taxon has been individually fit with a LOWESS line with a window of .75 for easier visualization of trend lines. Statistical differences are noted in Table 3.6.

Differences between bonobos and various common chimpanzee subspecies are much more common than differences among the common chimpanzee subspecies, and patterns of significant differences are not the same when analyzed between species and subspecies. Femur to humerus length ratio growth follows a similar trajectory among the three *P. troglodytes* subspecies, with little visual evidence to suggest that any individual taxon is closer to *P. paniscus*. However, ratio differences reach significance only for *P. t. verus* and *P. paniscus* in the adolescent age cohort (Figure 3.7). Ulna/radius length, which differs between *P. paniscus* and *P. troglodytes,* is here only significantly different between bonobos and *P. t. schweinfurthii* and *P. t. troglodytes* (Figure 3.7).

Tibia/femur, metatarsal/femur, and metacarpal/humerus length, which fail to reach significance when analyzed at the species level, are found to be different between bonobos and some individual subspecies. The tibia is longer relative to the femur in *P. t. troglodytes* compared to *P. paniscus* in the juvenile age class (Figure 3.7). Hand and foot bones (MC/H and MT/F) differ between *P. paniscus* and *P. t. troglodytes/P. t. schweinfurthii* respectively, although only in one age class each (Table 3.6), with bonobos having a relatively short metatarsal but relatively long metacarpal. Lastly, juvenile bonobos also have a significantly relatively shorter phalanx compared to the metacarpal than *P. t. troglodytes* juveniles.

In addition to these differences between *P. paniscus* and the individual *P. troglodytes* species, there is also one significant difference found between two *P. troglodytes* subspecies in radius/humerus length, which is higher in *P. t. troglodytes* juveniles compared to *P. t. verus*. Other variables are not found to differ between any groups.

Table 3.6 Significant post-hoc differences between taxa in lengths and length ratios

	Significant differences*	
	Juv	**Adol**
HLd	*P. t. t. > P. t. v*	
FLd/HLd		*P. p. > P. t. v.*
TLd/FLd	*P. p. < P. t. t.*	
RLd/HLd	*P. t. t. > P. t. v.*	
ULd/RLd	*P. p. < P. t. s. & P. t. t.*	*P. p. < P. t. s. & P. t. v.*
MCLd/HLd		*P.p. > P. t. t.*
MTLd/FLd	*P. p. < P. t. s.*	
PLd/MCLd	*P. p. < P. t. t.*	

**P. p. = P. paniscus; P. t. s. = P. t. schweinfurthii,P. t. t. = P. t. troglodytes, P. t. v. = P. t. verus*

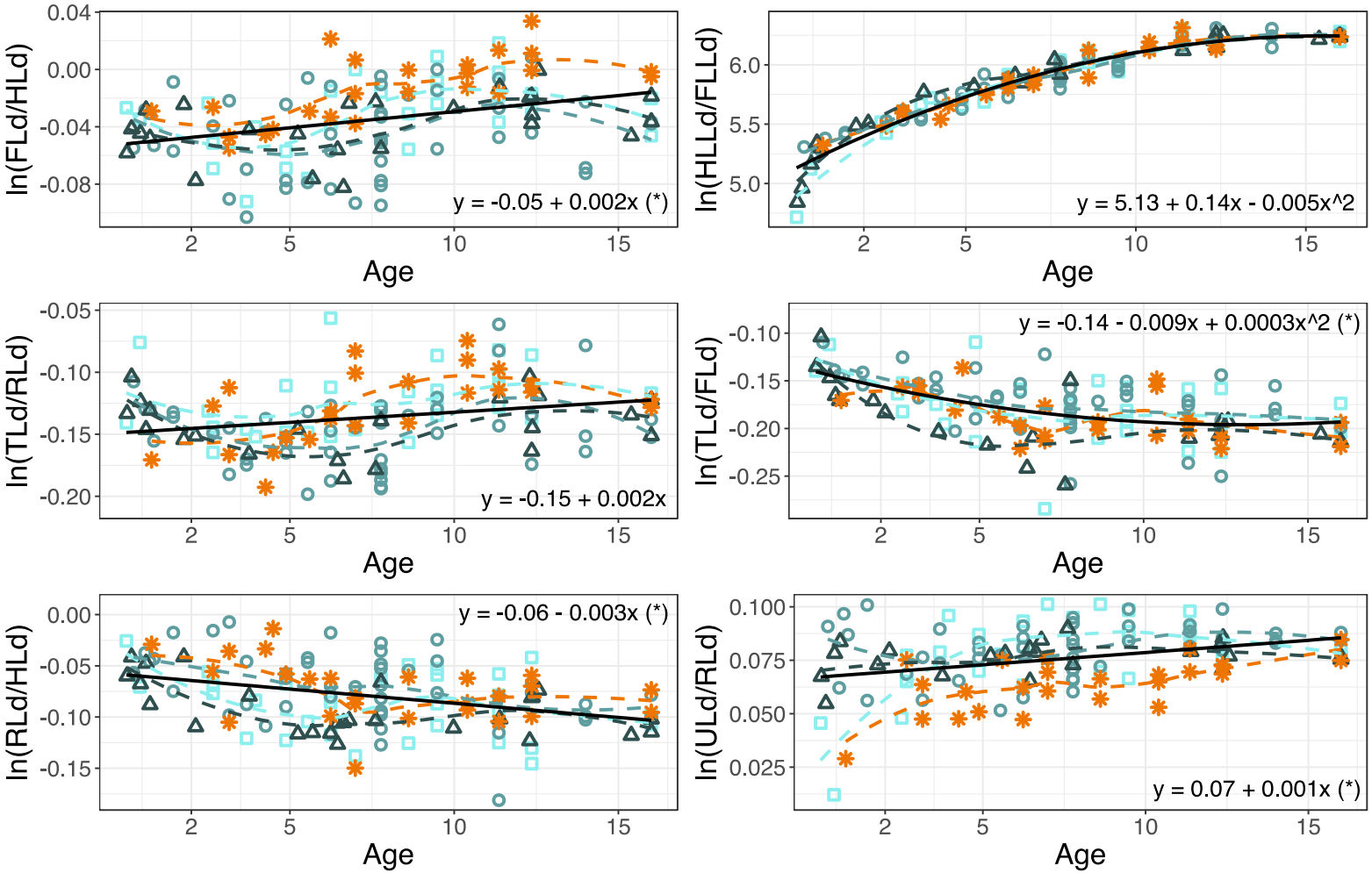

Figure 3.6 Change in length ratios in P. paniscus *and* P. troglodytes *subspecies.* P. paniscus = *orange stars,* P. troglodytes = *blue (*P. t. schweinfurthii = *squares,* P. t. troglodytes = *circles,* P. t. verus = *triangles). Black line = pooled total sample equation, dashed lines = LOWESS fits for visualization of taxon-specific trends. * indicates significant difference between taxa in one or more age groups.*

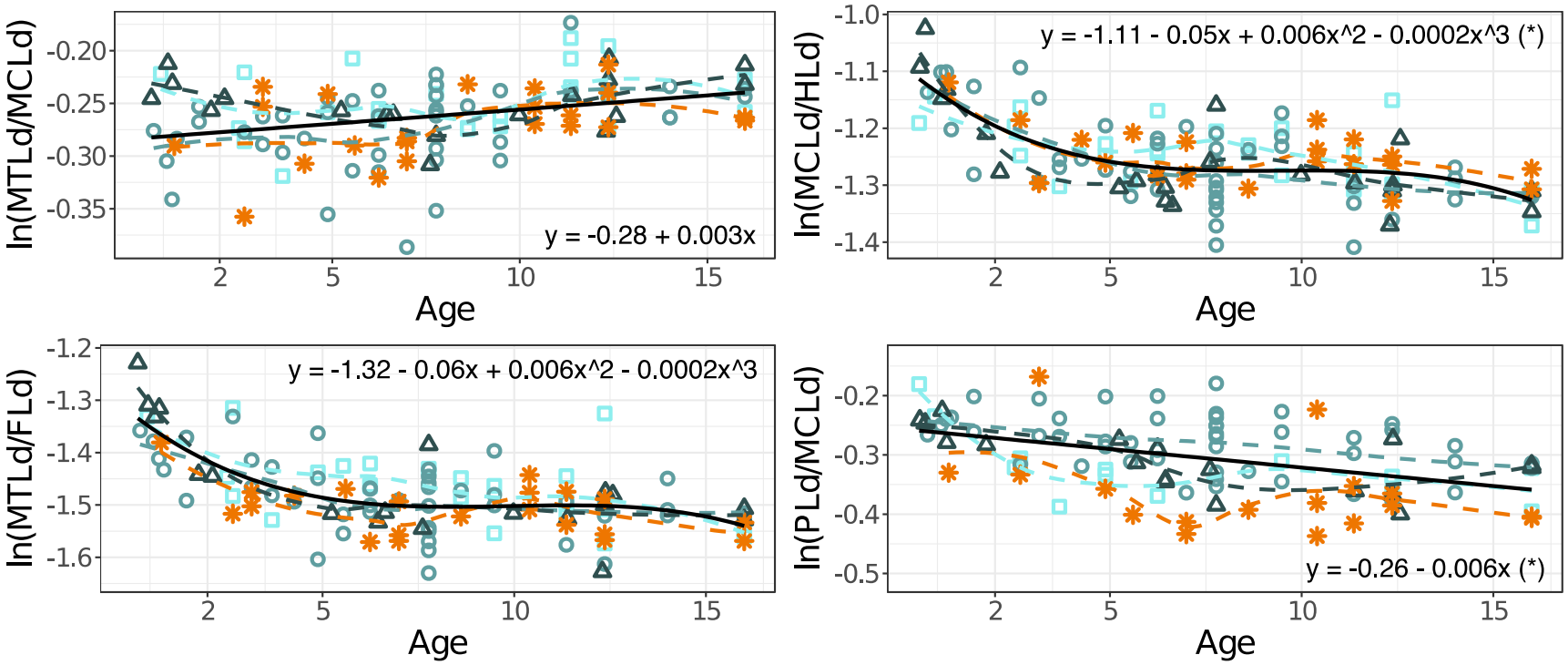

Figure 3.6 (cont'd).

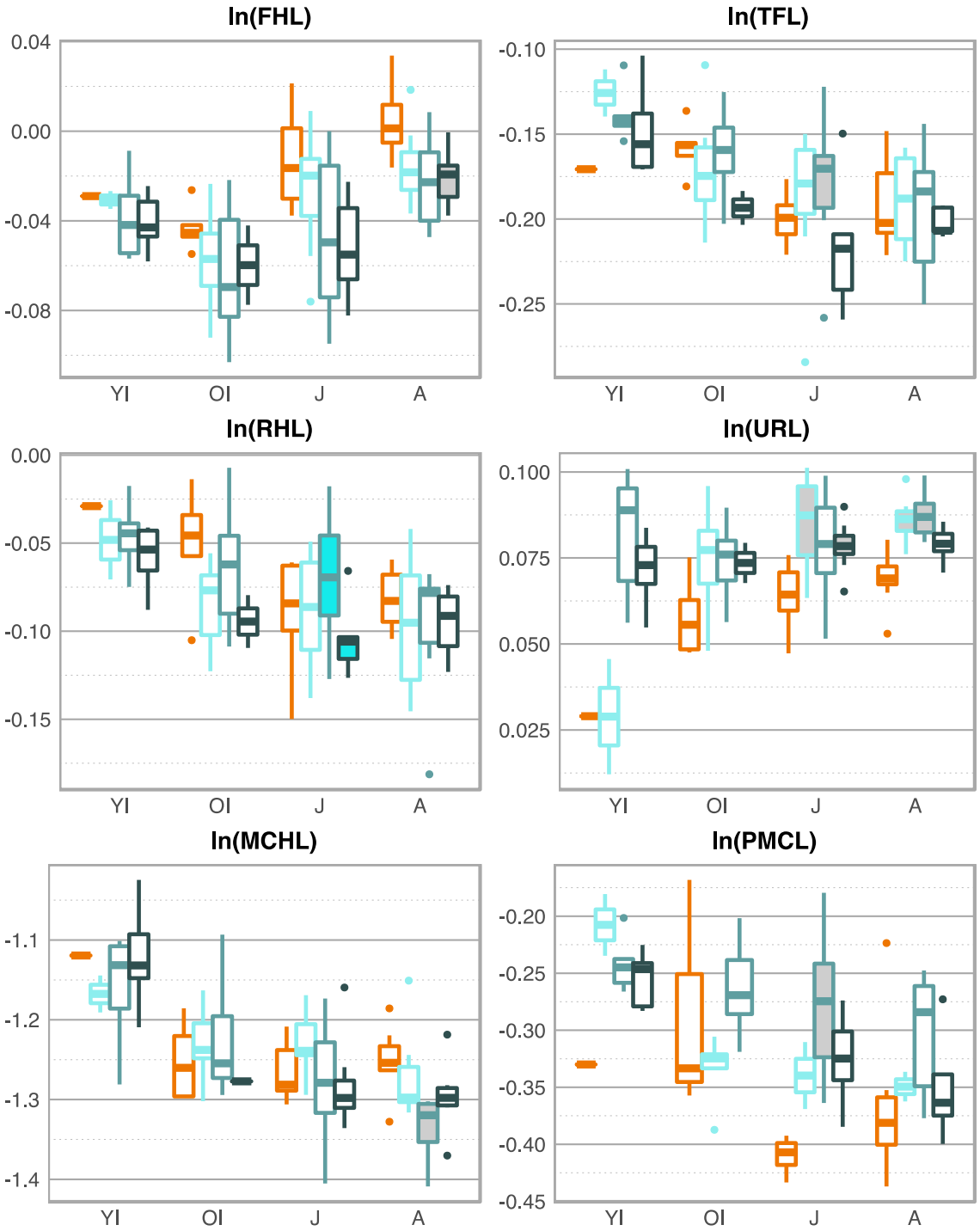

Figure 3.7 Selected box plots of limb bone ratios in the four non-adult age groups (YI = young infant, OI = old infant, J = juvenile, and A = adolescent). Grey fill = residuals from common line for P. troglodytes *subspecies significantly different from* P. paniscus *residuals; blue fill = residuals from common line for P. troglodytes subspecies significantly different from each other (not shown: HLd, MT/FLd). Color key same as previous.*

3.1.2.4 Summary

Despite significant differences in adults in some raw lengths (humerus and phalanx between species; humerus, phalanx, radius, and ulna between bonobos and some subspecies and between some subspecies), immature age groups do not differ systematically in these measurements. Bonobos and all common chimpanzees follow similar trajectories at least until around the adolescent age group (see Figure 3.5 for example), but unfortunately, data are too sparse to interpret patterns in the adolescent age range. Any systematic differences in dental development (leading to systematic bias of estimated ages) between bonobos and common chimpanzees could also bias these results, although for this to be a significant factor these differences would have to be larger than are indicated by currently available data. There are also no systematic differences among subspecies in raw diaphyseal lengths (the humerus, while it does reach significance transiently between two common chimpanzee subspecies, nevertheless does not appear to follow substantially different growth trajectories in these two groups).

Patterns are more complicated for length ratios. Inter-limb ratios such as femur/humerus length are significantly different between bonobos and common chimpanzee subspecies. There is no evidence for differences in femur/humerus length ratios between common chimpanzee subspecies during ontogeny. Differences between bonobos and common chimpanzees both as a group and in subspecies separately are apparent at early ages but do not reach significance until juveniles, and do not reach significance in comparisons with individual subspecies until adolescence.

Most intra-limb ratios did not show differences in adults, and most are also not different during ontogeny, but patterns are again slightly variable. Ulna/radius length

differed between adult *P. troglodytes* subspecies, in addition to bonobos and *P. t. troglodytes/P. t. verus*. Differences are also found during ontogeny, but not between the same taxa: bonobos appear to fall below common chimpanzees initially but converge on more similar values in adults, with significant differences found between bonobos and some common chimpanzees in juveniles and adolescents but no differences between *P. troglodytes* subspecies. Likewise, tibia/femur length, which is different between *P. t. schweinfurthii* and *P. t. verus* in adult males, transiently differs between *P. paniscus* and *P. t. troglodytes* during ontogeny (this may be driven by several low values for bonobos).

Hand and foot ratios were consistently different in adults: metatarsal/metacarpal, metatarsal/femur, and phalanx/metacarpal ratios all differed between species (and metatarsal/metacarpal and phalanx/metacarpal differed between bonobos and *P. t. troglodytes/P. t. verus* as well, with *P. t. schweinfurthii* intermediate between the two). Unlike femur/humerus length (another inter-limb ratio), metatarsal/metacarpal length was similar in all taxa during ontogeny, with bonobos and all subspecies fairly evenly scattered about the pooled sample line. Intra-limb ratios involving the metacarpal, metatarsal, and phalanx all show scattered significant differences between bonobos and single *P. troglodytes* subspecies in juveniles and adolescents. This appears to be reflective of underlying similarity between taxa in ratios of hand and foot metapodia to the more proximal limb elements, apparent from visual inspection of data scatters, although bonobos do tend to cluster below the pooled regression line for metatarsal/femur length. However, the lack of statistical significance of phalanx/metacarpal length is likely caused by a few high outlier values for *P. paniscus*, as other than these values, bonobos fall substantially below the common chimpanzee subspecies, consistent with the

differences found in adults. Thus, for femur/humerus and phalanx/metacarpal length, adult differences between bonobos and common chimpanzees appear to be a continuation of differences that are apparent from early in life. The opposite is true for ulna/radius length, in which lack of similarity in adults appears to be the product of convergence in values. Other differences are less systematic and less easily interpretable.

3.1.3 Comparison to behavioral data and Discussion

Based on the first prediction from hypothesis one, length ratios were expected to differ systematically between bonobo and common chimpanzees adults and to be similar between common chimpanzee subspecies, with these differences apparent from early in life. Length ratios were not expected to follow behavioral differences, in which *P. t. schweinfurthii* and *P. paniscus* tend to be more similar to one another in having relatively higher proportions of quadrupedalism compared to climbing and suspension than *P. t. verus* (the two *P. troglodytes* taxa significantly so) and the amount of quadrupedalism significantly increases with age (see Table 2.7, Table 2.8).

The main length ratio differences, as discussed above, are femur/humerus, phalanx/metacarpal, and ulna/radius length. Femur/humerus length is the only length ratio that completely follows predictions about adult differences, with bonobo adults significantly differing between common chimpanzees both as a group and as individual subspecies. Bonobos also differ from common chimpanzees in this ratio during ontogeny, although younger age groups do not reach statistical significance (see Discussion). In general, this pattern is consistent with genetic differences and is not consistent with behavioral data discussed above, because of the lack of morphological differences

between *P. troglodytes* subspecies both as adults and during ontogeny despite significant behavioral differences.

Phalanx/metacarpal length also differs between adults, but does not reach statistical significance between bonobos and *P. t. schweinfurthii*. However, this is probably due to small sample size in *P. t. schweinfurthii*: a scatterplot of metacarpal and phalanx length seems to show that they fall in with other *P. troglodytes* (Figure 3.8). This difference between taxa is also consistently exhibited throughout ontogeny, although relative phalanx length declines in all taxa and statistical significance is not always reached. This is consistent with the second prediction of hypothesis one and not consistent with behavioral differences exhibited during ontogeny. These results are consistent with previous studies suggesting that at broader taxonomic scales, having long phalanges relative to metapodials is associated with arboreal behavior, and that this ratio tends to decline with age (Young and Booth, 2016).

Lastly, ulna to radius length differed between adult *P. t. schweinfurthii* and *P. t. verus,* but also differed during ontogeny between *P. paniscus* and all *P. troglodytes* subspecies (not between any *P. troglodytes* subspecies). In contrast to femur/humerus length, bonobos actually appear to become more similar to *P. troglodytes* subspecies with age, rather than less, although differences are still significant in juveniles and adolescents (but not adults). This is difficult to reconcile with either genetic or behavioral data, as ontogenetic and adult data appear to be somewhat in contradiction. Although the difference is significant, it is quite small, and therefore may not be biomechanically meaningful. It is possible that these lengths in particular are impacted by the relative size

of the olecranon process of the ulna, which may be additionally reflective of muscle attachment rugosity. Further analyses will be necessary to address this question.

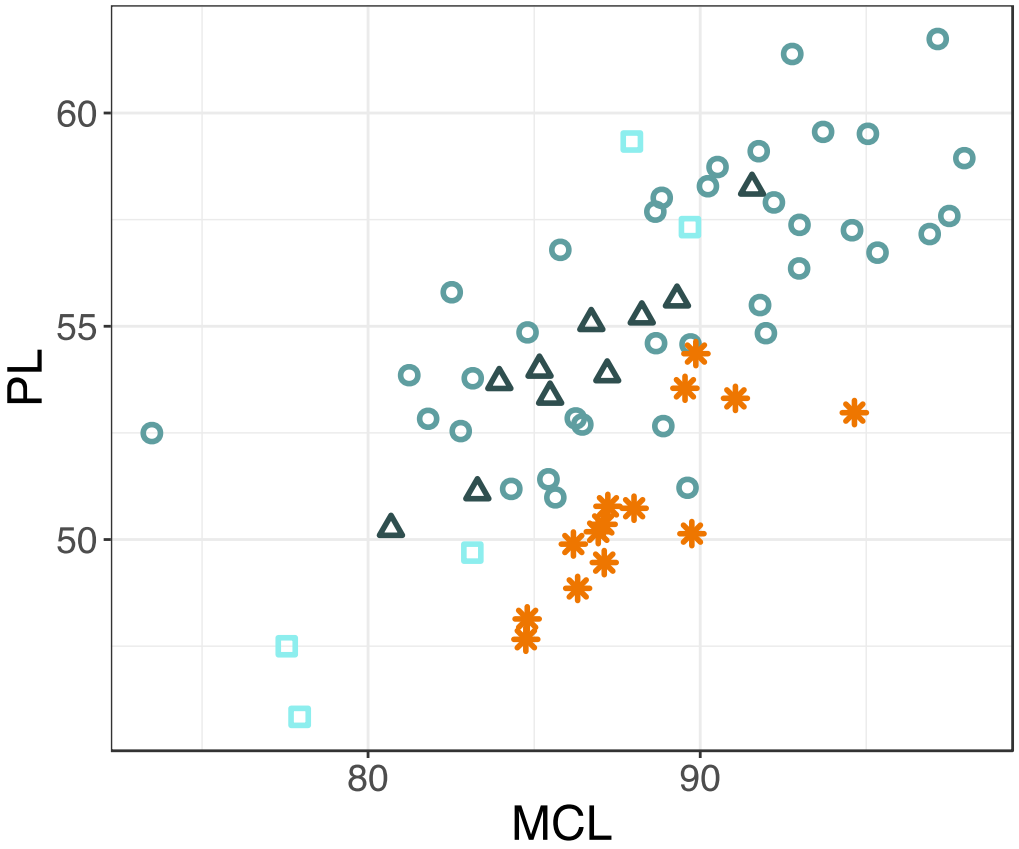

Figure 3.8 Phalanx and metacarpal length in adult Pan. P. paniscus = *orange stars,* P. troglodytes = *blue (*P. t. schweinfurthii = *squares,* P. t. troglodytes = *circles,* P. t. verus = *triangles)*

It is important to note that, outside of the relatively clear patterns noted above, there are a few other length proportions that differ between common chimpanzee subspecies as adults and, occasionally, during ontogeny. These are also difficult to align with predictions, as adult differences are not accompanied by ontogenetic differences, and vice versa. They may represent statistical error or artifacts of the relatively small sample sizes within each age group, and more data would be useful to further clarify

these issues. Nevertheless, where relatively clear patterns can be discerned, they generally seem to track systematic genetic differences between bonobos and common chimpanzees and are thus at least partially consistent with the hypothesis that length proportions are primarily genetically mediated.

3.2 CROSS-SECTIONAL GEOMETRY

The variables analyzed in this section are found in Table 3.7 and include inter- and intra-limb ratios of cross-sectional strength (Zp), ratios describing bone shape (Zx/Zy), and bone cross-sectional strength scaled by body mass*bone length. As previously, ratios were natural log-transformed prior to analyses for methodological considerations, and raw variables were also natural log-transformed for adults for statistical reasons but were analyzed in unlogged space for ontogenetic comparisons because statistics for these do not assume normality.

Table 3.7 Strength, strength ratio, and cross-sectional area variables

Variable	Abbreviation
Measures of bone strength*	
Femur to humerus Zp	FHZp
Tibia to radius Zp	TRZp
Tibia to femur Zp	TFZp
Radius to humerus Zp	RHZp
Ulna to radius Zp	URZp
3rd metatarsal to 3rd metacarpal Zp	MTMCZp
3rd metacarpal to humerus Zp	MCHZp
3rd metatarsal to femur Zp	MTFZp
Scaled Zp†	[*]Zp/(BM*BL)
Measures of bone shape and area*	
Bone shape (Zx/Zy)	[*]ZxZy

** Ratios natural logged for all analyses*

*** Calculated for each bone. [*] in abbreviation replaced by relevant bone letter code (F = Femur, T = Tibia, H = Humerus, R = Radius, U = Ulna, MC = 3rd metacarpal, MT = 3rd metatarsal)*

† Scaled cross sections are divided by the product of estimated body mass (BM) and relevant bone length (BL) (see text).

3.2.1 Adults

3.2.1.1 Species-level analyses

Summary statistics (means and standard deviations) for adult strengths and strength ratios within species can be found in Table 3.8. Prior to analysis, sex differences were tested with two sample t-tests with unequal variance or Mann-Whitney U tests with Bonferroni-corrected significance levels ($\alpha < .05/2$). These results are found in the summary statistics tables referenced above. Only tibia shape (TZxZy) is significantly different between sexes in bonobos. In common chimpanzees as a group, ulna/radius Zp, scaled ulna Zp, and humerus shape (HZxZy) are different between sexes, as well as virtually all measures of total, cortical, and percent cortical area (but not marrow cavity area).

Accordingly, for species-level analyses, sexes were pooled for all measures of cross-sectional strength (Zp) except for ulna/radius and scaled ulna Zp. For measures of shape, sexes were pooled for all analyses except for tibia and humerus.

Table 3.8 Summary statistics for inter-bone strength ratios, scaled Zp's, and shape ratios, by species and sex

	P. paniscus						***P. troglodytes***					
	Male			**Female**			**Male**			**Female**		
Variable**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**
FHZp	9	0.397	0.137	10	0.354	0.067	29	0.247	0.094	42	0.291	0.095
TRZp*	9	1.146	0.184	10	0.949	0.104	29	0.766	0.120	43	0.745	0.139
TFZp*	9	-0.533	0.152	10	-0.682	0.093	31	-0.691	0.145	42	-0.781	0.128
RHZp*	9	-1.283	0.091	10	-1.276	0.081	28	-1.220	0.147	43	-1.235	0.115
URZp	9	0.154	0.155	10	0.079	0.102	28	**0.043**	0.162	42	**-0.064**	0.165
MTMCZp	7	-0.519	0.209	10	-0.523	0.128	26	-0.425	0.121	36	-0.419	0.136
MCHZp	7	-2.452	0.128	10	-2.464	0.214	25	-2.585	0.097	37	-2.542	0.156
MTRZp	7	-3.351	0.250	10	-3.341	0.219	25	-3.254	0.158	38	-3.249	0.189
FZp/ (BM*BL)	9	-1.908	0.117	10	-1.852	0.136	31	-1.824	0.156	42	-1.813	0.180
HZp/ (BM*BL)	9	-2.306	0.182	10	-2.212	0.106	29	-2.114	0.157	42	-2.137	0.173
TZp/ (BM*BL)*	9	-2.248	0.222	10	-2.315	0.120	31	-2.316	0.200	43	-2.385	0.190
RZp/ (BM*BL)	9	-3.516	0.203	10	-3.393	0.149	29	-3.240	0.200	41	-3.275	0.228
UZp/ (BM*BL)	9	-3.437	0.192	10	-3.398	0.107	28	**-3.273**	0.222	40	**-3.428**	0.226
MCZp/ (BM*BL)	7	-3.473	0.149	10	-3.368	0.279	27	-3.360	0.154	37	-3.364	0.190
MTZp/ (BM*BL)	7	-3.728	0.162	10	-3.625	0.246	25	-3.562	0.150	38	-3.549	0.186
FZxZy	9	0.969	0.078	10	0.943	0.038	31	0.853	0.090	42	0.873	0.083
HZxZy	9	1.038	0.092	10	1.105	0.068	29	**0.998**	0.070	43	**1.044**	0.045
TZxZy	9	**1.588**	0.142	10	**1.406**	0.125	31	1.499	0.155	43	1.424	0.141
RZxZy	9	0.982	0.064	10	0.993	0.045	29	1.025	0.078	44	1.008	0.071
UZxZy	9	0.976	0.096	10	0.930	0.094	28	0.987	0.108	42	0.961	0.090
MCZxZy	7	1.044	0.079	10	1.041	0.052	28	1.057	0.085	37	1.040	0.079
MTZxZy	7	1.357	0.091	10	1.316	0.068	26	1.339	0.093	39	1.322	0.094

Bold values are significantly different between males and females within species

** Not normally distributed; see text for details of analysis*

*** all variables natural logged for analysis*

The figures below show box and whisker plots for all variables analyzed (Figure 3.9 through Figure 3.11), with results of statistical comparisons between species. Species differences were tested with two sample t-tests with unequal variance if variables were normally distributed or Mann-Whitney U tests if not (see tables). For comparisons in separate sexes, significance levels were Bonferroni adjusted ($\alpha < .05/2$).

In inter-bone strength ratios, *P. paniscus* have significantly higher femur/humerus, tibia/radius, and tibia/femur ratios than *P. troglodytes*, and bonobo females also have higher ulna/radius Zp. The reverse is true for metatarsal/metacarpal, in which *P. troglodytes* have a relatively stronger metatarsal compared to their metacarpal than bonobos. In scaled cross-sectional strength, *P. troglodytes* are significantly higher than bonobos in the humerus, radius, and metatarsal. In measures of cross-sectional shape, bonobos have higher femoral Zx/Zy ratios (i.e., a more AP strengthened femur) than common chimpanzees. The same is true for the humerus in bonobo and common chimpanzee females, but not males.

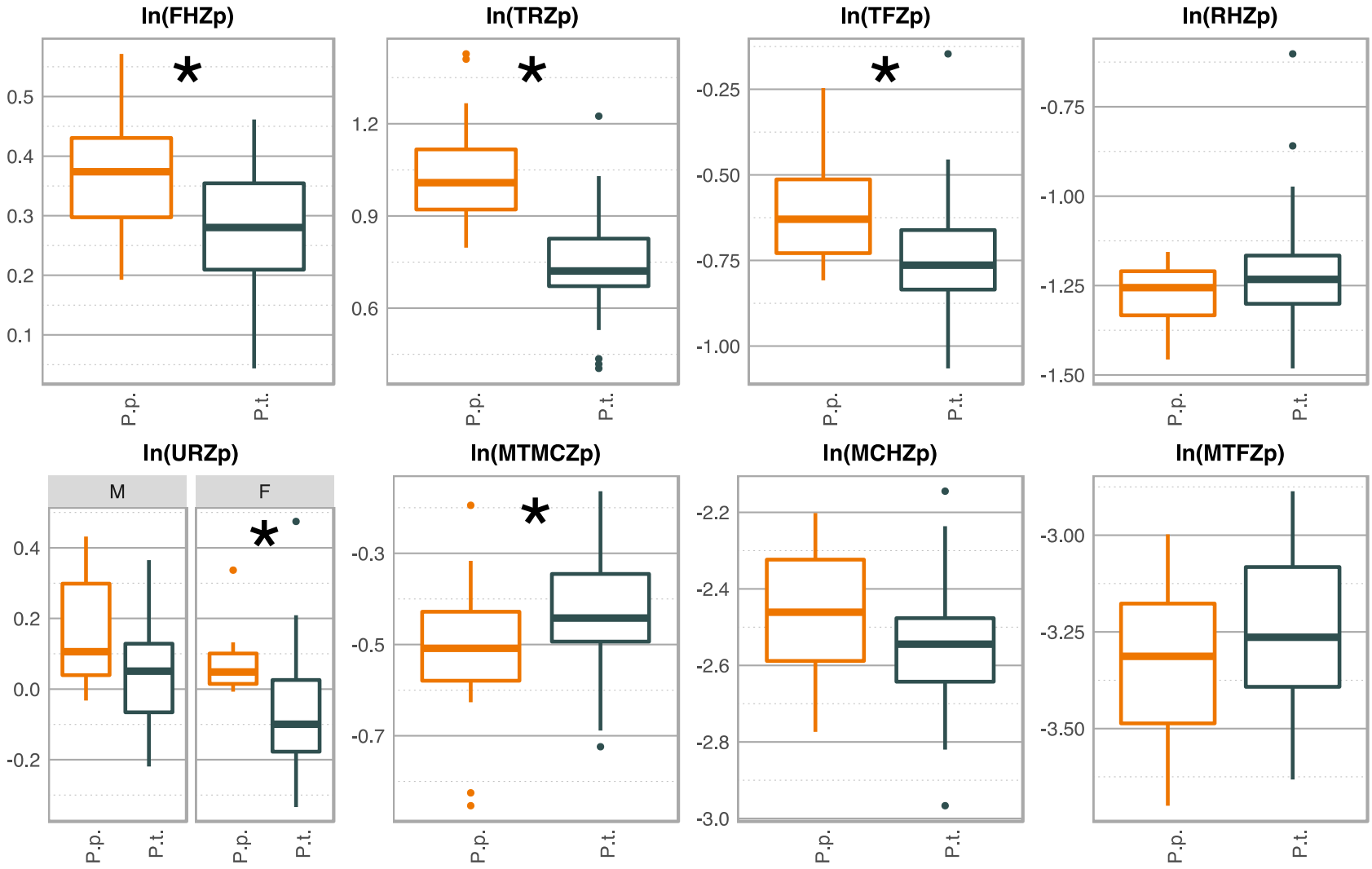

Figure 3.9 Cross-sectional shape ratios in adult P. paniscus *(P.p.) and* P. troglodytes *(P.t.). Asterisks indicate significant differences.*

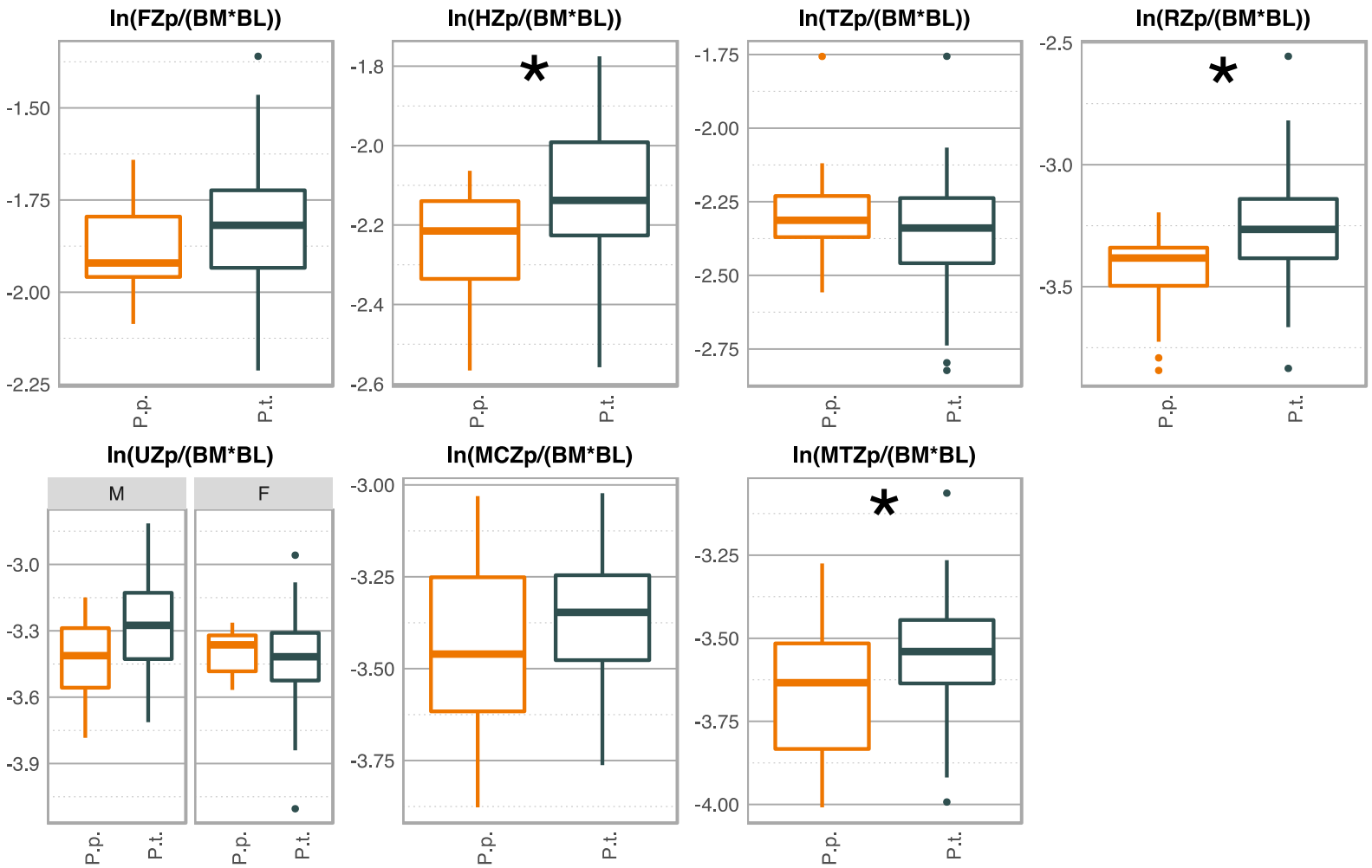

Figure 3.10 Scaled cross-sectional strength in adult P. paniscus *(P.p.) and* P. troglodytes *(P.t.) Asterisks indicate significant differences.*

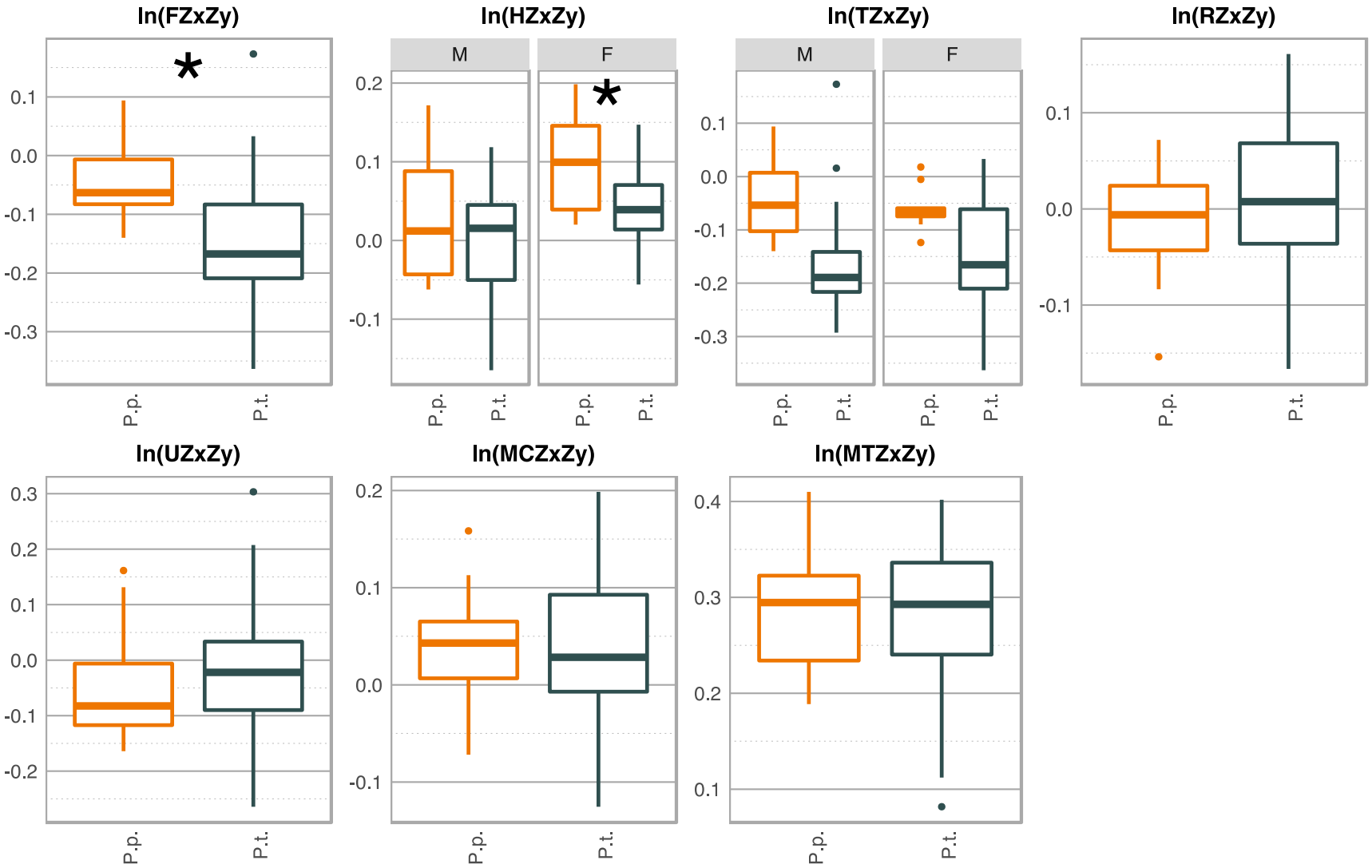

Figure 3.11 Shape ratios in adult P. paniscus *(P.p.) and* P. troglodytes *(P.t.). Asterisks indicate significant differences.*

3.2.1.2 Subspecies-level analyses

Again, sex differences were tested with two sample t-tests with unequal variance or Mann-Whitney U tests with Bonferroni-corrected significance levels prior to analysis, with results reported in summary statistics Table 3.9 with a family-wise error rate of .0167 (bonobos were again not included in this analysis as they have been previously analyzed). Patterns of sex differences are slightly different than those in *P. troglodytes* as a whole: scaled ulnar Zp is still significantly higher in females than in males, but only in *P. t. troglodytes*, but ulna to radius Zp does not reach statistical significance in any individual subspecies. There are additional differences in tibia and metatarsal shape ratios between sexes in *P. t. verus*, with the former being significantly higher in males and the latter lower. Accordingly, analyses in this section take place on pooled sex samples, except for scaled ulna Zp, tibia and metatarsal shape.

Table 3.9 Summary statistics for and sex differences in strength, scaled Zp's, and shape ratios (species)

	P. t. schwein.						***P. t. trog.***						***P. t. verus***					
	Male			**Female**			**Male**			**Female**			**Male**			**Female**		
Variable	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**
FHZp	3	0.351	0.090	8	0.322	0.100	18	0.228	0.091	19	0.297	0.085	8	0.250	0.086	15	0.268	0.106
TRZp*	3	0.849	0.156	8	0.726	0.152	18	0.757	0.124	19	0.817	0.142	8	0.754	0.102	16	0.668	0.076
TFZp*	3	-0.745	0.145	8	-0.849	0.072	18	-0.688	0.166	19	-0.762	0.122	10	-0.679	0.111	15	-0.769	0.153
RHZp*	3	-1.242	0.219	8	-1.252	0.157	18	-1.216	0.164	19	-1.282	0.096	7	-1.218	0.074	16	-1.170	0.084
URZp*	2	0.289	0.096	8	0.053	0.234	18	0.061	0.147	19	-0.028	0.138	8	-0.060	0.131	15	-0.172	0.074
MTMCZp	2	-0.428	0.049	7	-0.406	0.196	17	-0.398	0.139	19	-0.401	0.134	7	-0.489	0.046	10	-0.463	0.086
MCHZp	2	-2.631	0.164	7	-2.550	0.105	18	-2.585	0.103	19	-2.563	0.162	5	-2.566	0.052	11	-2.500	0.176
MTRZp	2	-3.398	0.239	7	-3.265	0.269	17	-3.222	0.164	19	-3.260	0.165	6	-3.297	0.091	12	-3.223	0.187
FZp/(BM*BL)	3	-1.681	0.084	8	-1.782	0.229	18	-1.860	0.173	19	-1.853	0.169	10	-1.801	0.118	15	-1.779	0.167
HZp/(BM*BL)	3	-2.079	0.124	8	-2.125	0.170	18	-2.126	0.162	19	-2.188	0.190	8	-2.101	0.173	15	-2.078	0.140
TZp/(BM*BL)*	3	-2.252	0.086	8	-2.427	0.225	18	-2.353	0.220	19	-2.418	0.217	10	-2.267	0.183	16	-2.325	0.120
RZp/(BM*BL)	3	-3.224	0.153	8	-3.270	0.270	18	-3.263	0.230	19	-3.371	0.215	8	-3.193	0.143	14	-3.146	0.158
UZp/(BM*BL)	2	-2.930	0.164	8	-3.294	0.280	18	**-3.286**	0.222	19	**-3.487**	0.226	8	-3.329	0.171	13	-3.423	0.162
MCZp/(BM*BL)	2	-3.282	0.147	7	-3.372	0.181	18	-3.395	0.155	19	-3.435	0.176	7	-3.294	0.141	11	-3.237	0.166
MTZp/(BM*BL)	2	-3.483	0.044	7	-3.520	0.319	17	-3.572	0.166	19	-3.591	0.157	6	-3.558	0.126	12	-3.498	0.115
FZxZy	3	0.901	0.054	8	0.931	0.058	18	0.844	0.078	19	0.890	0.087	10	0.857	0.118	15	0.819	0.059
HZxZy	3	0.932	0.078	8	1.036	0.043	18	0.996	0.065	19	1.037	0.055	8	1.026	0.070	16	1.056	0.029
TZxZy	3	1.661	0.270	8	1.351	0.108	18	1.473	0.154	19	1.503	0.142	10	**1.496**	0.095	16	**1.367**	0.108
RZxZy	3	0.951	0.023	8	1.002	0.046	18	1.015	0.078	19	0.982	0.071	8	1.076	0.064	17	1.038	0.072
UZxZy	2	1.102	0.182	8	1.021	0.074	18	1.006	0.093	19	0.949	0.095	8	0.915	0.095	15	0.945	0.083
MCZxZy	2	1.109	0.116	7	1.019	0.065	18	1.049	0.077	19	1.040	0.093	8	1.060	0.104	11	1.052	0.061
MTZxZy	2	1.385	0.099	7	1.309	0.103	17	1.373	0.074	19	1.307	0.113	7	**1.245**	0.074	13	**1.351**	0.046

Bold values are significantly different between males and females within subspecies

** Not normally distributed and/or unequal variance; see text for details of analysis*

Box and whisker plots along with significant post-hoc comparisons for the variables analyzed are shown in Figure 3.12 through Figure 3.14. Significant differences were tested with one-way ANOVA if variables were normally distributed with equal variance or Kruskal-Wallis tests if not (noted in summary statistics tables). All post-hoc comparisons used Games-Howell tests at a family-wise error rate of .05. For comparisons in males and females separately, these significance levels were adjusted to keep the family-wise error rate at .05.

In bone strength ratios, overall differences between the four taxa are found in all except the metatarsal/femur and metacarpal/humerus ratios, and post-hoc tests find significant differences in all ratios except those involving the hand and foot bones (Figure 3.12). Femur to humerus strength is significantly higher in bonobos than in *P. t. troglodytes* or *P. t. verus*, with *P. t. schweinfurthii* somewhat intermediate. Tibia to radius and tibia to femur strength are both significantly higher in bonobos than in all three *P. troglodytes*, and tibia/radius strength also differs between *P. t. troglodytes* and *P. t. verus*. Radius to humerus strength is higher in *P. t. verus* than *P. paniscus*, and ulna/radius strength is lower in *P. t. verus* than all three other taxa.

Measures of scaled Zp's (Figure 3.13) show a significant effect of taxon in the humerus, radius, ulna (males only), metacarpal, and metatarsal. Of these, *post hoc* comparisons find that bonobos have significantly lower values than *P. t. verus* for the humerus and radius, and also that bonobos have lower values than *P. t. schweinfurthii* and that *P. troglodytes* had lower values than *P. t. verus* for scaled radius Zp. *Post hoc* tests find no significant differences for scaled ulna Zp between *P. paniscus*, *P. t. troglodytes*, and *P. t. verus*; male *P. t. schweinfurthii* clearly have much higher values

than any of these taxa, although sample sizes are too small for statistical testing. Differences are also found in scaled metacarpal strength between *P. t. troglodytes* and *P. t. verus*, with significantly higher values in the latter.

Shape ratios (Figure 3.14) show overall differences in the femur, humerus, tibia (females), ulna, and metatarsal (males). *Post hoc* comparisons show that *P. paniscus* and *P. t. schweinfurthii* each show significant differences in femoral shape with *P. t. troglodytes* and *P. t. verus.* Bonobos have the highest shape ratios (i.e., more A-P strengthened femora), and values decline from *P. t. schweinfurthii* to *P. t. troglodytes* to *P. t. verus*. In contrast, in the humerus, bonobos have significantly higher humerus Zx/Zy only compared to *P. t. schweinfurthii*. In tibial Zx/Zy, *P. t. verus* females have significantly lower values than *P. t. troglodytes* females, with the same true in males for metatarsal shape. Lastly, in the ulna, *P. t. schweinfurthii* has somewhat higher Zx/Zy values than the other taxa, reaching statistical significance in comparisons with *P. paniscus* and *P. t. verus*.

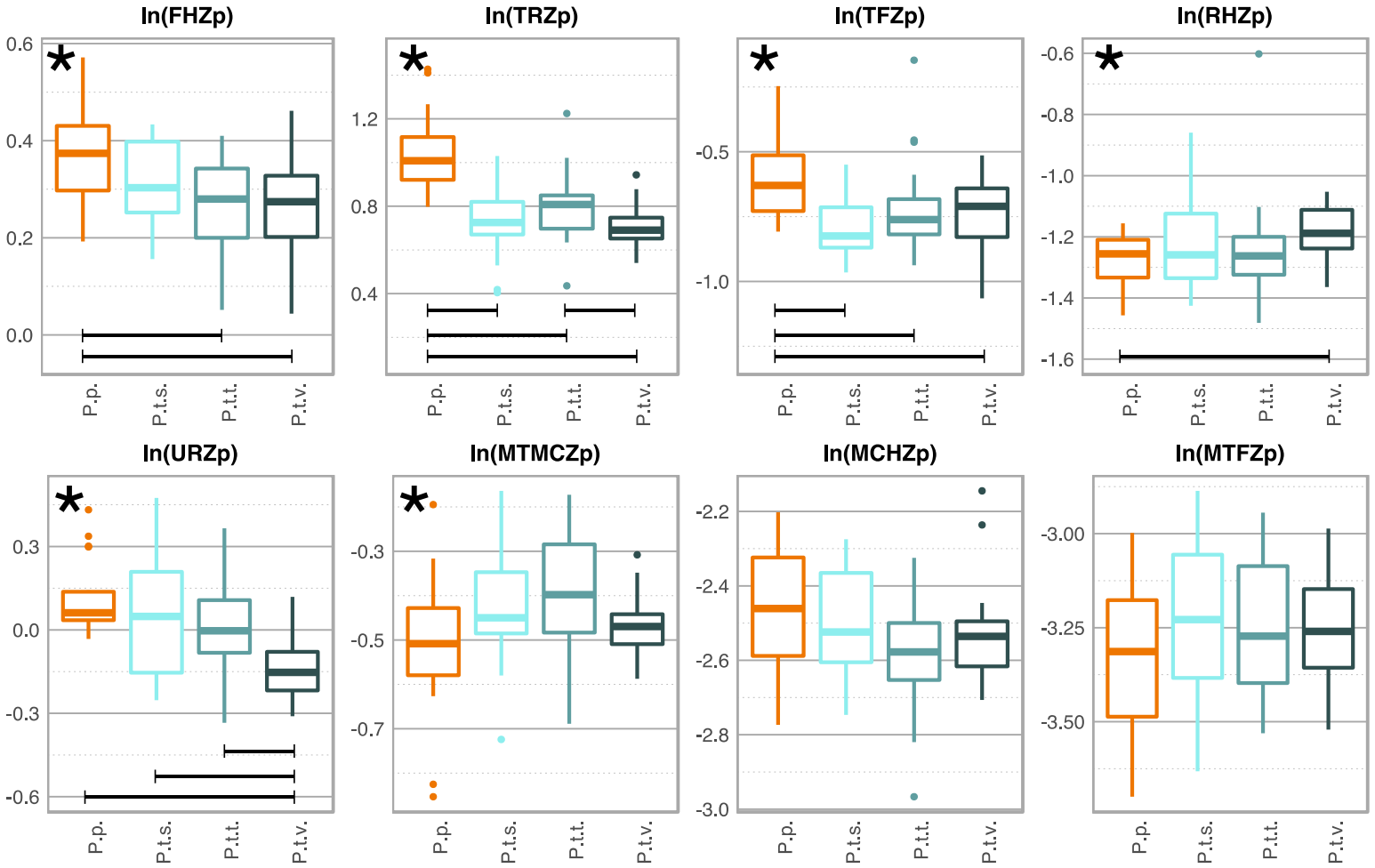

Figure 3.12 Cross-sectional strength ratios in adult P. paniscus *(P.p.),* P. t. schweinfurthii *(P.t.s.),* P. t. troglodytes *(P.t.t.), and* P. t. verus *(P.t.v.). Significant overall differences between taxa (within sexes) are indicated with large black asterisks; significant post-hoc comparisons are indicated with brackets.*

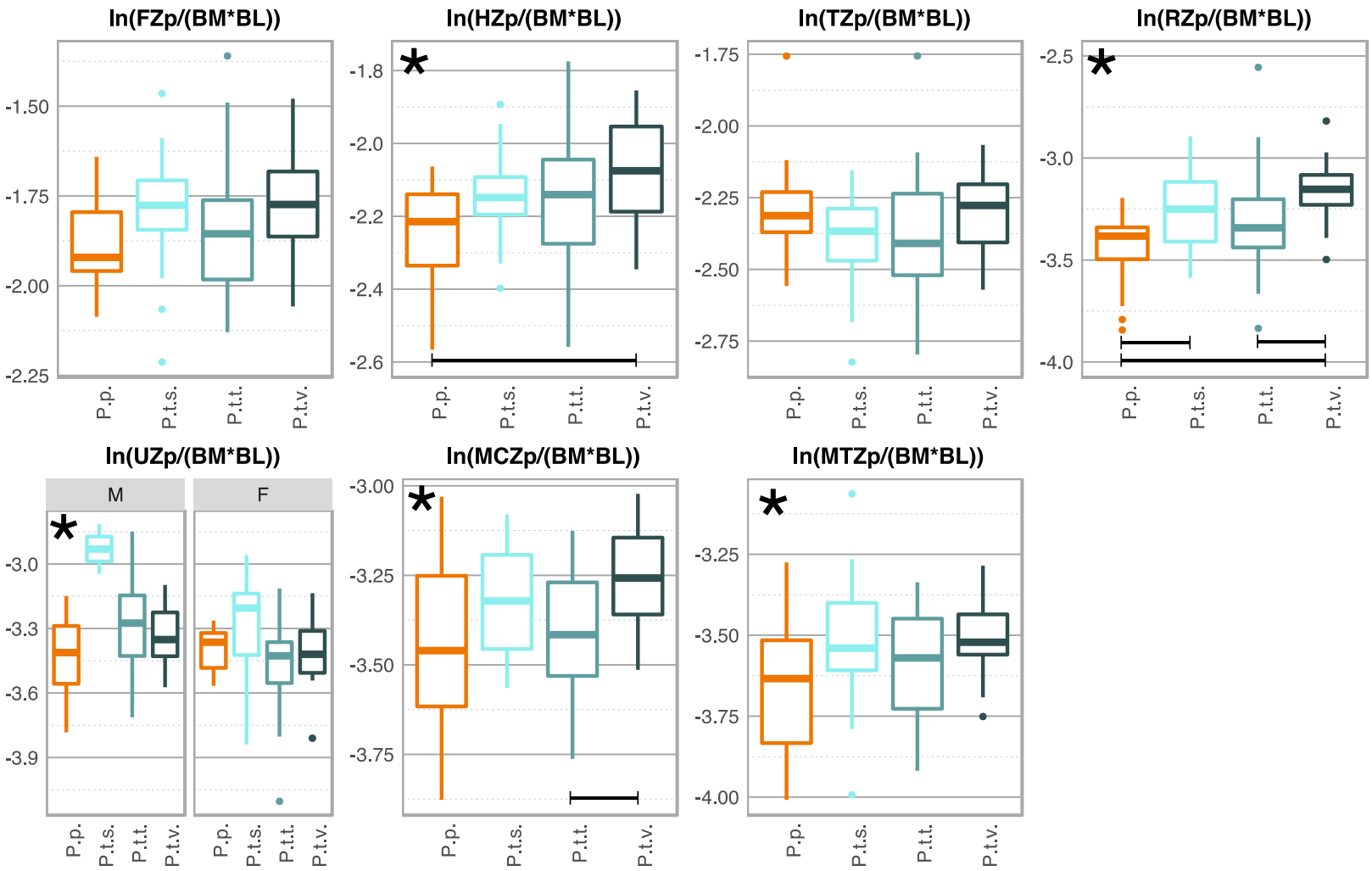

Figure 3.13 Scaled cross-sectional strength in adult P. paniscus *(P.p.),* P. t. schweinfurthii *(P.t.s.),* P. t. troglodytes *(P.t.t.), and* P. t. verus *(P.t.v.). Significant overall differences between taxa (within sexes) are indicated with large black asterisks; significant post-hoc comparisons are indicated with brackets.*

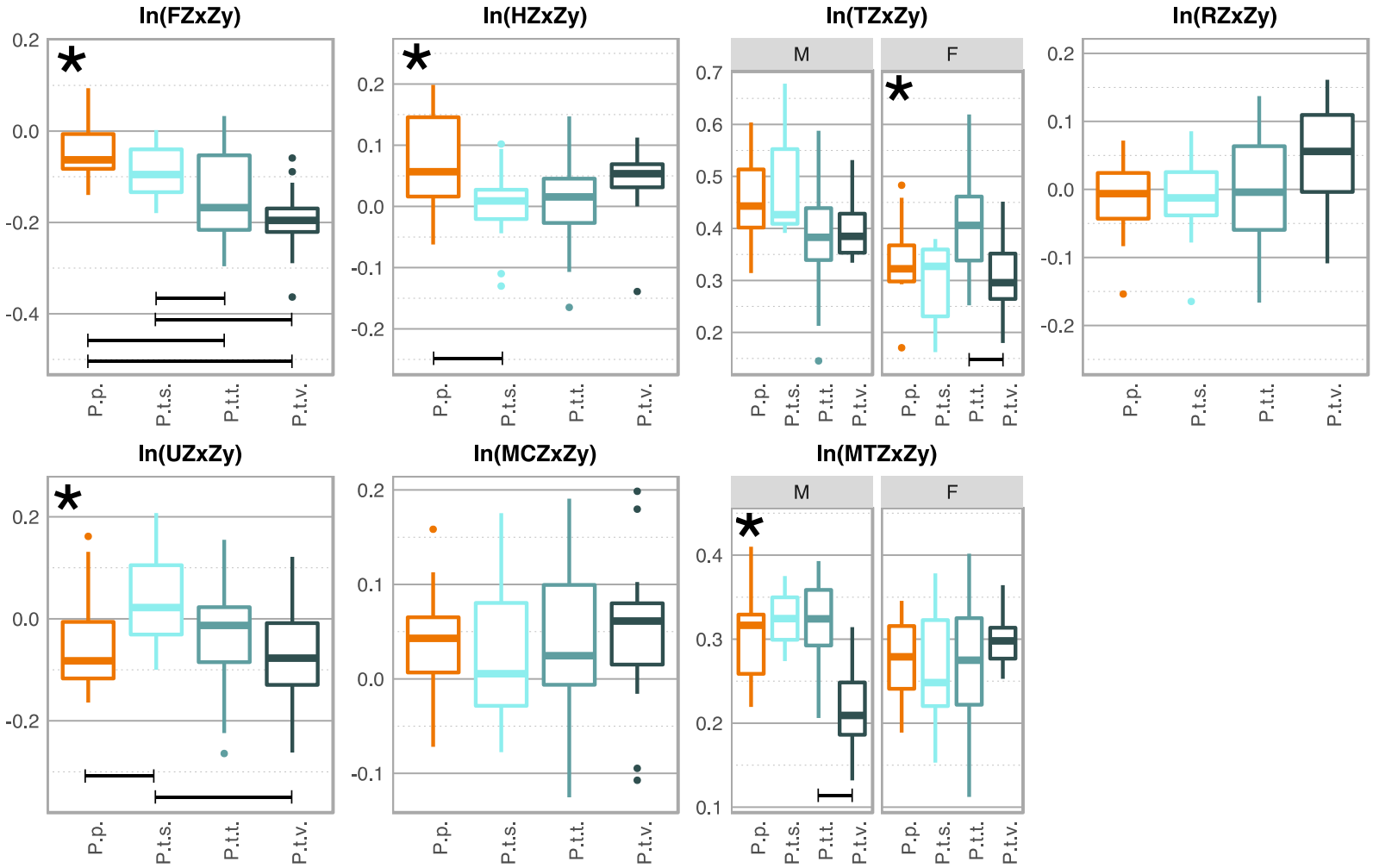

Figure 3.14 Shape ratios in adult P. paniscus *(P.p.),* P. t. schweinfurthii *(P.t.s.),* P. t. troglodytes *(P.t.t.), and* P. t. verus *(P.t.v.). Significant overall differences between taxa (within sexes) are indicated with large black asterisks; significant post-hoc comparisons are indicated with brackets.*

3.2.1.3 Summary

Cross-sectional strength and shape parameters vary both between adult *P. paniscus* and *P. troglodytes* and among *P. paniscus* and adult *P. troglodytes* subspecies. Often, differences that are significant between bonobos and *P. troglodytes* as a group were not found to vary significantly between bonobos and each *P. troglodytes* subspecies individually. Overall, more variation was found among *P. troglodytes* subspecies in cross-sectional geometry than in the bone lengths and length ratios discussed in the previous section. Femur to humerus strength was found to be higher in bonobos than in *P. troglodytes* in general, but was only significantly different between bonobos and *P. t. troglodytes*/*verus*, and not *P. t. schweinfurthii*. Tibia/radius and tibia/femur Zp differed between bonobos and all three subspecies as well as *P. troglodytes* pooled (higher in bonobos). In the case of metatarsal/metacarpal strength, the reverse is true: although values for bonobos are lower than *P. troglodytes* as a whole, no significant differences were found with individual subspecies. *P. t. verus* also showed differences from several other *P. troglodytes* subspecies, with lower tibia/radius and ulna/radius strengths than some or all other taxa.

Some of these patterns can be clarified by looking at scaled cross-sectional strength measurements. At the species level, there are no differences in scaled femoral strength, but scaled humeral strength is lower in bonobos than in common chimpanzees. This suggests that the relatively longer femur of bonobos cannot entirely be responsible for their higher femoral relative to humeral strength, and that lower humeral strength may rather be driving these patterns (however, most differences with individual subspecies fail to reach significance). Likewise, differences in ulna/radius strength may be driven by

underlying differences in relative radius strength, which differs both between bonobos and *P. t. verus/P. t. schweinfurthii* and between *P. t. troglodytes* and *P. t. verus*, while ulnar strength is more similar between taxa (with the exception of male *P. t. schweinfurthii*).

Lastly, bonobos also had higher femur and humerus shape ratios than *P. troglodytes* as a whole and than *P. troglodytes* subspecies. The femur showed some of the clearest differences between taxa: bonobos had the highest values and the least M-L widened femora (ratios closest to zero), with values declining from *P. t. schweinfurthii* to *P. t. troglodytes* to *P. t. verus*; significant differences were found between both bonobos and *P. t. schweinfurthii*, respectively, and the other two subspecies. Again, there were also several differences between *P. troglodytes* subspecies: *P. t. schweinfurthii* had higher ulnar shape ratios than both *P. paniscus* and *P. t. verus*, and male *P. t. verus* had lower metatarsal shape ratios than *P. t. troglodytes*.

3.2.2 Ontogenetic

3.2.2.1 Overall correlations with age

Spearman correlations for each variable with age are found in Table 3.10. One *P. t. schweinfurthii* (RMCA 13094) had abnormally high marrow cavity areas and low cortical areas (with CA's around 50% of the next lowest values and MA's between 1.3 and 3 times as large), but with similar total areas, which could be a result of age or a nutritional deficit or other pathological condition. To be conservative, this individual was therefore excluded from these and all subsequent analyses even though external dimensions and other measurements of cross-sectional geometry were normal.

All inter-bone cross-sectional strength ratios are significantly correlated with age in at least one taxon except for tibia/femur Zp. Femur/humerus, tibia/radius, radius/humerus, and metatarsal/femur strength ratios are significantly correlated with age in all species and subspecies examined. The direction of change is constant across taxa but differs depending on the bones involved: ratios of radius to humerus and metacarpal to humerus in the forelimb and metatarsal to femur in the hind limb decrease with age, but all others increase with age. In contrast, all scaled measurements of bone cross-sectional strength decrease with age in all taxa (even though femur, tibia, and ulna scaled Zp's do not reach statistical significance in some individual subspecies, Table 3.10).

Of all bone shape measurements, only the femur, tibia, radius, and ulna change significantly with age. The femur and tibia change in opposite directions, with the tibia becoming more A-P strengthened (higher Zx relative to Zy), and the femur becoming relatively more M-L strengthened (the reverse). Correlations are significant in all taxa for the tibia but not in *P. t. troglodytes* for the femur. The radius and ulna show less consistent patterns, with correlations significant only in individual subspecies (Table 3.10).

As with other skeletal dimensions, polynomial models (with the correct order of the polynomial determined in forward stepwise fashion) were used to further examine age-related changes within species and subspecies.

Table 3.10 Correlations and significance for cross-sectional strength ratios, scaled Zp's, and cross-sectional shape ratios with age

	P. paniscus	***P. troglodytes***	***P. t. schwein.***	***P. t. trog.***	***P. t. verus***
Variable	**rho***	**rho**	**rho**	**rho**	**rho**
FHZp	**0.47**	**0.69**	**0.63**	**0.70**	**0.80**
TRZp	**0.74**	**0.73**	**0.71**	**0.74**	**0.78**
TFZp	0.11	0.16	0.25	0.07	0.28
RHZp	**-0.40**	**-0.39**	**-0.43**	**-0.37**	**-0.42**
URZp	0.00	**0.57**	**0.45**	**0.55**	**0.66**
MTMCZp	0.39	**0.42**	0.15	**0.58**	**0.47**
MCHZp	**-0.70**	**-0.40**	**-0.51**	**-0.48**	-0.30
MTRZp	**-0.55**	**-0.55**	**-0.55**	**-0.49**	**-0.61**
FZp/(BM*BL)	**-0.59**	**-0.37**	-0.34	-0.26	**-0.55**
HZp/(BM*BL)	**-0.64**	**-0.51**	**-0.50**	**-0.41**	**-0.66**
TZp/(BM*BL)	**-0.58**	**-0.25**	-0.18	-0.12	**-0.50**
RZp/(BM*BL)	**-0.71**	**-0.56**	**-0.52**	**-0.51**	**-0.78**
UZp/(BM*BL)	**-0.61**	**-0.39**	-0.34	**-0.29**	**-0.57**
MCZp/(BM*BL)	**-0.70**	**-0.58**	**-0.65**	**-0.49**	**-0.56**
MTZp/(BM*BL)	**-0.77**	**-0.53**	**-0.55**	**-0.44**	**-0.52**
FZxZy	**-0.66**	**-0.48**	-0.21	**-0.51**	**-0.74**
HZxZy	-0.23	0.00	0.15	0.06	-0.23
TZxZy	**0.72**	**0.80**	**0.75**	**0.84**	**0.87**
RZxZy	-0.35	0.16	**0.50**	0.01	0.17
UZxZy	-0.35	**-0.20**	0.03	-0.14	**-0.54**
MCZxZy	-0.18	-0.16	-0.09	-0.21	-0.14
MTZxZy	0.35	0.18	0.04	0.28	0.12

3.2.2.2 Species-level analyses

To examine species-level differences, bonobo residuals from a polynomial fit to the pooled chimpanzee sample were calculated, and Wilcox rank-sum tests were then used to test whether these residuals significantly differed from zero within each age category (except Young Infants; see Methods). Because adult differences were tested in the previous section, references in this section refer to the non-adult age cohorts. Species means and standard deviations in each age group, along with statistical significance of differences between species, are found in Table 3.11.

As with lengths, bonobos and common chimpanzees seem to follow broadly similar ontogenetic trajectories in all cross-sectional variables. Intra-limb bone strength ratios are best fit with first order polynomials, except for ulna/radius strength, which is best fit by a second order polynomial. Inter-limb ratios require either second order (metatarsal/metacarpal and tibia/radius) or third order (femur/humerus) polynomials. Bonobos and common chimpanzees are not significantly different in either of the infant age groups. In both femur/humerus and tibia/radius strength, bonobos and common chimpanzees are more similar at earlier ages but diverge, reaching statistical significance in juveniles and/or adolescents (Table 3.11). Although adolescent bonobos have significantly lower metacarpal/humerus strength than common chimpanzees, mean values in younger age cohorts are actually more disparate than those in older with bonobos having relatively higher values (Table 3.11), i.e., the two taxa become more similar with age.

Scaled bone strengths are best fit by first order polynomials for all bones except the radius and humerus, which are best fit by fourth order polynomial equations, and

values decreased with age for all bones (with more drastic decreases generally occurring between younger age cohorts). In general, the two species are similar until after about five years of age; no comparisons are significant in juveniles, but in adolescents, scaled cross-sectional strength is higher in *P. troglodytes* in all bones except the tibia and ulna. In bone cross-sectional shape, all best fit lines are first order polynomials and there are no significant differences between species in any age cohort.

Table 3.11 Means and (SD)'s of cross-sectional strength ratios within each age cohort

	Young Inf. (0-2y)				Old Inf. (2-5y)			
	P. pan.		*P. trog.*		*P. pan.*		*P. trog.*	
Variable	*n*	*mean(SD)*	*n*	*mean(SD)*	*n*	*mean(SD)*	*n*	*mean(SD)*
FHZp	1	-0.066 (NA)	13	-0.081 (0.155)	5	0.209 (0.102)	18	0.092 (0.083)
TRZp	1	0.480 (NA)	13	0.218 (0.208)	6	0.727 (0.139)	18	0.440 (0.155)
TFZp	1	-0.579 (NA)	13	-0.750 (0.097)	5	-0.598 (0.244)	18	-0.733 (0.128)
RHZp	1	-1.124 (NA)	13	-1.049 (0.169)	6	-1.099 (0.116)	18	-1.081 (0.206)
URZp	1	-0.203 (NA)	12	-0.321 (0.181)	5	0.051 (0.154)	18	-0.191 (0.168)
MTMCZp	1	-0.960 (NA)	11	-0.605 (0.129)	4	-0.571 (0.035)	15	-0.532 (0.176)
MCHZp	1	-1.840 (NA)	12	-2.278 (0.164)	4	-2.057 (0.101)	15	-2.295 (0.184)
MTRZp	1	-2.735 (NA)	12	-2.821 (0.143)	3	-2.913 (0.173)	15	-2.919 (0.259)
FZp/(BM*BL)	1	-1.659 (NA)	13	-1.311 (0.283)	5	-1.687 (0.257)	18	-1.641 (0.195)
HZp/(BM*BL)	1	-1.622 (NA)	13	-1.268 (0.348)	6	-1.909 (0.281)	18	-1.793 (0.249)
TZp/(BM*BL)	1	-2.067 (NA)	13	-1.919 (0.236)	6	-2.079 (0.293)	18	-2.206 (0.228)
RZp/(BM*BL)	1	-2.717 (NA)	13	-2.265 (0.349)	6	-2.958 (0.255)	18	-2.799 (0.315)
UZp/(BM*BL)	1	-2.949 (NA)	12	-2.685 (0.309)	5	-3.003 (0.344)	18	-3.064 (0.255)
MCZp/(BM*BL)	1	-2.343 (NA)	12	-2.444 (0.269)	4	-2.815 (0.286)	15	-2.835 (0.276)
MTZp/(BM*BL)	1	-3.013 (NA)	12	-2.811 (0.182)	4	-3.102 (0.307)	15	-3.092 (0.266)

	Juv. (5-10y)				Adol. (10-14y)			
FHZp	8	**0.359 (0.126)**	41	**0.190 (0.104)**	8	**0.375 (0.078)**	20	**0.216 (0.097)**
TRZp	8	**0.841 (0.052)**	39	**0.707 (0.152)**	7	0.886 (0.113)	18	0.809 (0.144)
TFZp	8	-0.667 (0.104)	39	-0.654 (0.201)	7	-0.640 (0.072)	18	-0.644 (0.144)
RHZp	8	-1.149 (0.060)	43	-1.163 (0.207)	8	-1.148 (0.093)	19	-1.235 (0.164)
URZp	8	0.076 (0.123)	41	-0.039 (0.168)	8	-0.075 (0.108)	17	-0.022 (0.155)
MTMCZp	6	-0.401 (0.161)	34	-0.444 (0.111)	8	-0.454 (0.064)	18	-0.462 (0.204)
MCHZp	6	-2.241 (0.189)	39	-2.378 (0.150)	8	**-2.284 (0.055)**	19	**-2.433 (0.144)**
MTRZp	6	-3.041 (0.232)	34	-3.001 (0.187)	8	-3.113 (0.045)	18	-3.109 (0.200)
FZp/(BM*BL)	8	-1.828 (0.254)	41	-1.576 (0.183)	8	**-2.109 (0.141)**	18	**-1.606 (0.322)**
HZp/(BM*BL)	8	-2.200 (0.280)	43	-1.807 (0.216)	8	**-2.481 (0.136)**	18	**-1.846 (0.343)**
TZp/(BM*BL)	8	-2.295 (0.308)	39	-2.046 (0.270)	7	-2.568 (0.152)	17	-2.062 (0.359)
RZp/(BM*BL)	8	-3.261 (0.305)	43	-2.888 (0.304)	8	**-3.548 (0.201)**	18	**-2.980 (0.391)**
UZp/(BM*BL)	8	-3.248 (0.355)	40	-3.003 (0.247)	8	-3.691 (0.223)	16	-3.102 (0.362)
MCZp/(BM*BL)	6	-3.198 (0.373)	39	-2.917 (0.198)	8	**-3.514 (0.172)**	18	**-2.980 (0.358)**
MTZp/(BM*BL)	6	-3.313 (0.306)	34	-3.084 (0.242)	8	**-3.716 (0.137)**	17	**-3.241 (0.367)**

Bold values significantly different between species at alpha of .05

Table 3.11, cont'd

	Young Inf. (0-2y)				Old Inf. (2-5y)			
	P. pan.		***P. trog.***		***P. pan.***		***P. trog.***	
Variable	*n*	*mean(SD)*	*n*	*mean(SD)*	*n*	*mean(SD)*	*n*	*mean(SD)*
FZxZy	1	1.144 (NA)	13	1.000 (0.050)	5	1.079 (0.054)	18	0.976 (0.053)
HZxZy	1	1.112 (NA)	13	0.997 (0.070)	6	1.115 (0.070)	18	1.050 (0.076)
TZxZy	1	1.175 (NA)	13	1.100 (0.085)	6	1.271 (0.039)	18	1.207 (0.095)
RZxZy	1	0.978 (NA)	13	0.970 (0.077)	6	1.042 (0.099)	18	0.976 (0.080)
UZxZy	1	0.886 (NA)	12	1.078 (0.074)	5	1.162 (0.096)	18	1.017 (0.070)
MCZxZy	1	1.114 (NA)	12	1.036 (0.082)	4	1.041 (0.087)	15	1.038 (0.089)
MTZxZy	1	1.438 (NA)	12	1.272 (0.076)	4	1.254 (0.114)	15	1.272 (0.119)
	Juv. (5-10y)				**Adol. (10-14y)**			
FZxZy	8	0.988 (0.069)	41	0.942 (0.067)	8	0.939 (0.092)	20	0.914 (0.069)
HZxZy	8	1.100 (0.068)	44	1.043 (0.059)	8	1.081 (0.057)	20	1.038 (0.064)
TZxZy	8	1.384 (0.079)	39	1.368 (0.119)	7	1.426 (0.062)	18	1.503 (0.117)
RZxZy	8	0.985 (0.102)	43	0.959 (0.078)	8	0.921 (0.056)	19	1.021 (0.083)
UZxZy	8	1.004 (0.111)	41	1.071 (0.107)	8	1.006 (0.070)	18	1.024 (0.096)
MCZxZy	6	1.104 (0.094)	39	0.967 (0.080)	8	1.034 (0.072)	19	0.977 (0.067)
MTZxZy	6	1.332 (0.063)	34	1.321 (0.122)	8	1.443 (0.101)	18	1.320 (0.105)

Bold values significantly different between species at alpha of .05

3.2.2.3 Subspecies-level analyses

LOWESS fits were used to visually assess subspecies growth trends in cross-sectional parameters. These were statistically tested using residuals for each subspecies (and bonobos) from a pooled polynomial regression line fit to the entire data scatter with Bonferroni adjusted pairwise Wilcox rank-sum tests within each age group. Again, as adult differences were tested in the previous section, this section is in reference to the non-adult ages only. See the previous section for description of the orders of the best-fit polynomial models for each of the bone parameters.

Plots for cross-sectional strength ratios are found in Figure 3.15, with summary statistics included in the Appendix. Both femur/humerus and tibia/radius ratios show

increases with age in all taxa. In the former, the young infant bonobo falls with common chimpanzees and values seem to diverge from there, reaching statistical significance in adolescents along the same taxonomic lines as found in adults (Table 3.12), although mean values for bonobos are higher than those for the other subspecies in the younger age groups as well (Figure 3.16). (It is important to note that this may be related to sampling effects across age groups). A slightly different pattern is found in tibia/radius: bonobos again have higher ratios than the other taxa, but the greatest difference occurs in the old infant age group (Table 3.12, Figure 3.16). Ulna/radius strength also increases with age and shows the only other statistical difference between taxa and the only statistical difference in cross-sectional strength between two *P. troglodytes* subspecies: *P. t. verus* have significantly lower values in the juvenile age group than both *P. t. schweinfurthii* and *P. t. troglodytes* (Table 3.12, Figure 3.16). Other inter-limb ratios (radius/humerus and tibia/femur, not shown) remain relatively constant or slightly decrease with age but show little evidence for taxonomic differences.

Like other inter-limb ratios, metatarsal/metacarpal strength ratios increase with age, but there are no obvious statistical or visual differences between any of the taxa (Figure 3.15). However, both the metatarsal and metacarpal become relatively less strong with age compared to the more proximal limb elements. In the former, taxa are similar, but in the latter, as discussed in the previous section, there are larger visual differences among infants, with bonobos having the relatively strongest metacarpals and *P. t. verus* the weakest, and taxa become more similar with age (Figure 3.16); however, these differences do not reach statistical significance.

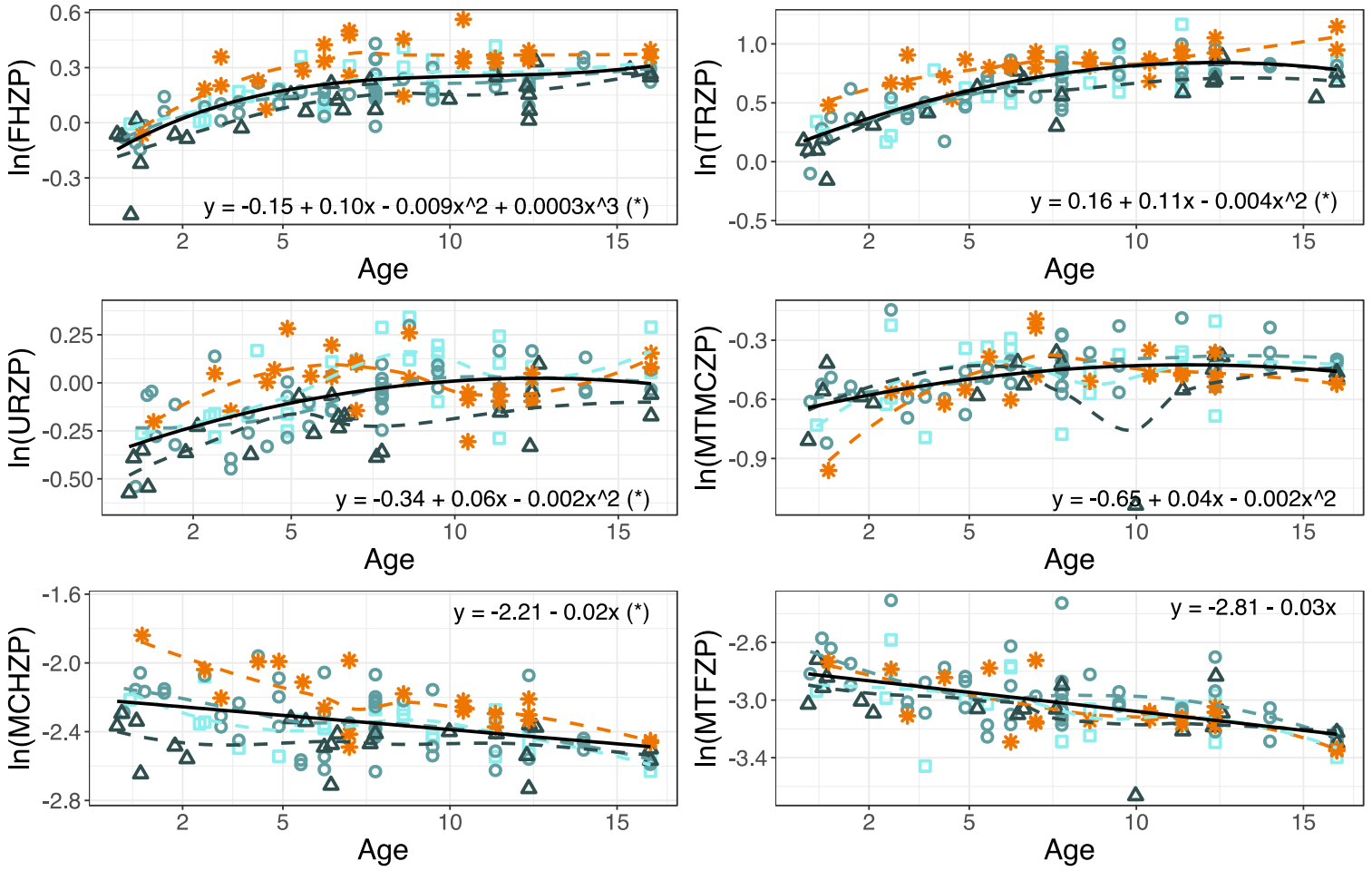

Figure 3.15 Growth in strength ratios in P. paniscus *and* P. troglodytes *subspecies.* P. paniscus = *orange stars,* P. troglodytes = *blue (*P. t. schweinfurthii = *squares,* P. t. troglodytes = *circles,* P. t. verus = *triangles). Black line = pooled total sample equation, dashed lines = LOWESS fits for visualization of taxon-specific trends. * indicates significant difference between taxa in one or more age groups. Not included: tibia/femur and radius/humerus strength. See Table 3.12 for post-hoc differences.*

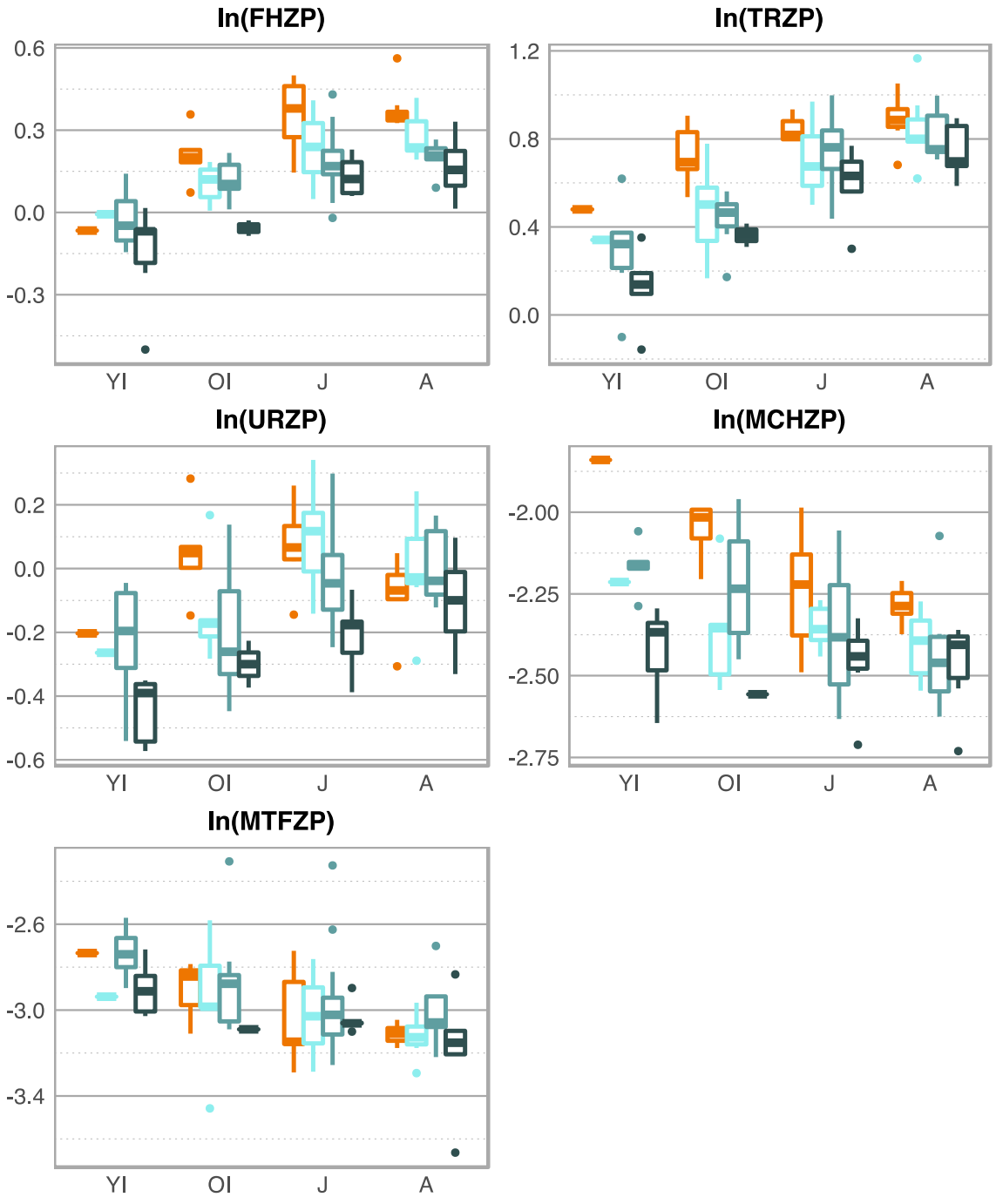

Figure 3.16 Selected box plots of limb bone strength ratio residuals in the four non-adult age groups (YI = young infant, OI = old infant, J = juvenile, and A = adolescent). See Table 3.12 for significant post-hoc differences between taxa within each age group. Color key same as previous.

Scaled Zp's universally decline with age in all taxa and (although some bones are best fit by simple linear models); this decline seems to be most rapid during infancy, prior to two years of age (Figure 3.17). Values are generally similar in both the infant age groups, but from there, bonobos diverge from the rest of common chimpanzees. Bonobos have a significantly relatively weaker humerus and radius than at least one subspecies in juveniles, and by adolescence, have lower values than at least one subspecies for all bones (or, for the femur and humerus, than all three subspecies; Table 3.12, Figure 3.17, Figure 3.18). In the adolescent age group, *P. t. schweinfurthii* are generally intermediate in value between *P. paniscus* and *P. troglodytes*, but closer to the former, and are usually not significantly different from either (except for femur and humerus, as noted above). The exception is scaled tibia strength, which is never significantly different.

Table 3.12 Post-hoc differences in cross-sectional properties within age groups

Variable	Old inf	Juv	Adol
FHZP			*P.p./P.t.t. & P.t.v.*
TRZP	*P.p./P.t.t.**		
URZP		*P.t.v./P.p. & P.t.s.*	
FZp/(BM*BL)			*P.p./P.t.s. & P.t.t. & P.t.v.*
HZp/(BM*BL)		*P.p./P.t.s. & P.t.t.*	*P.p./P.t.s. & P.t.t. & P.t.v.*
RZp/(BM*BL)		*P.p./P.t.v.*	*P.p./P.t.v.; P.t.s./P.t.v.*
UZp/(BM*BL)			*P.p./P.t.t.*
MCZp/(BM*BL)			*P.p./P.t.t. & P.t.v.*
MTZp/(BM*BL)			*P.p./P.t.t.*
FZxZy		*P.t.v./P.t.s. & P.t.t.*	
HZxZy		*P.t.s./P.t.v.*	

**P p=P. paniscus; P.t.s.=P. t. schweinfurthii,P. t. t. = P. t. troglodytes, P. t. v. = P. t. verus*

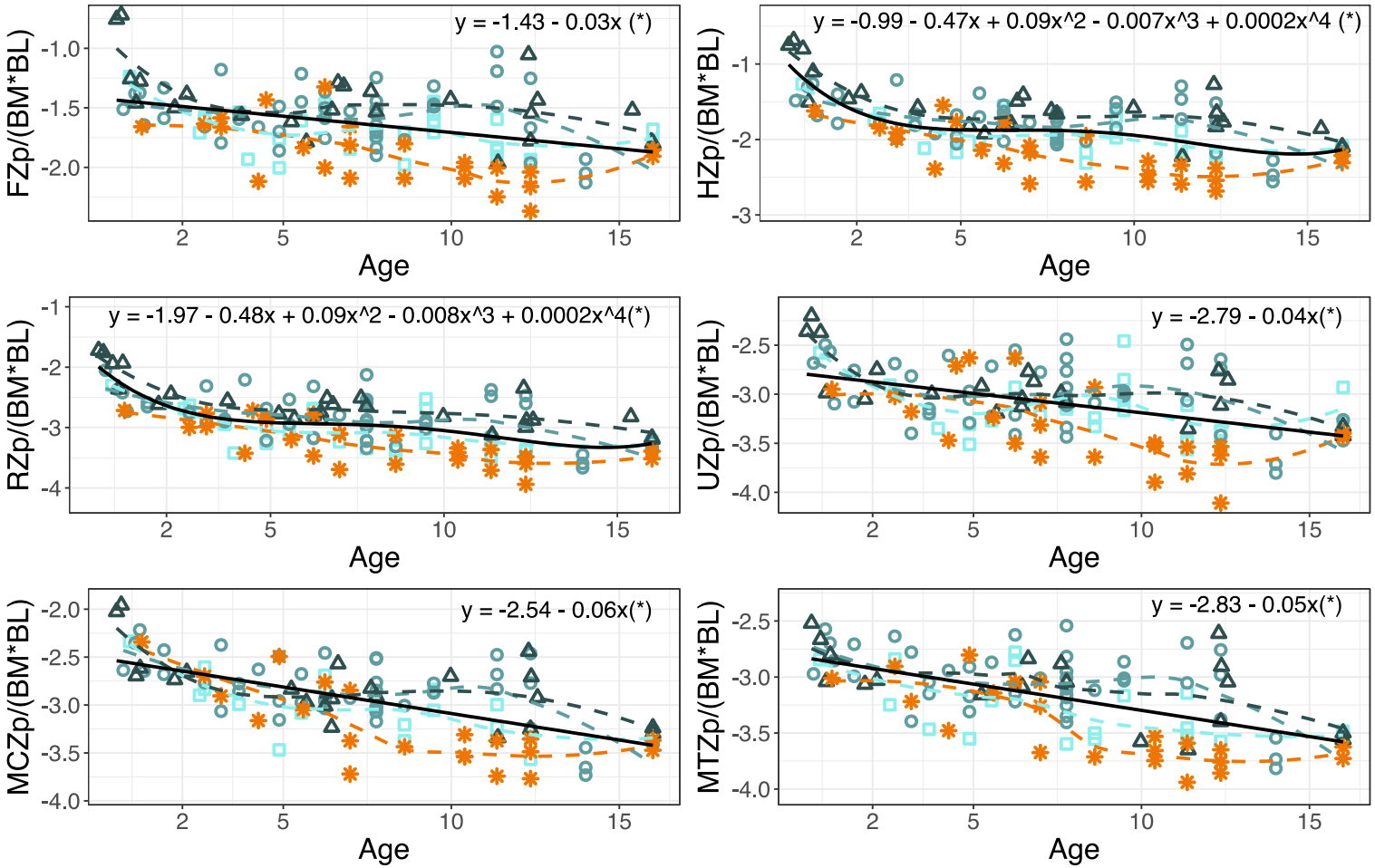

Figure 3.17 Growth in scaled Zp's in P. paniscus *and* P. troglodytes *subspecies.* P. paniscus = *orange stars,* P. troglodytes = *blue (*P. t. schweinfurthii = *squares,* P. t. troglodytes = *circles,* P. t. verus = *triangles). Black line = pooled total sample equation, dashed lines = LOWESS fits for visualization of taxon-specific trends. * indicates significant difference between taxa in one or more age groups. Not included: tibia.*

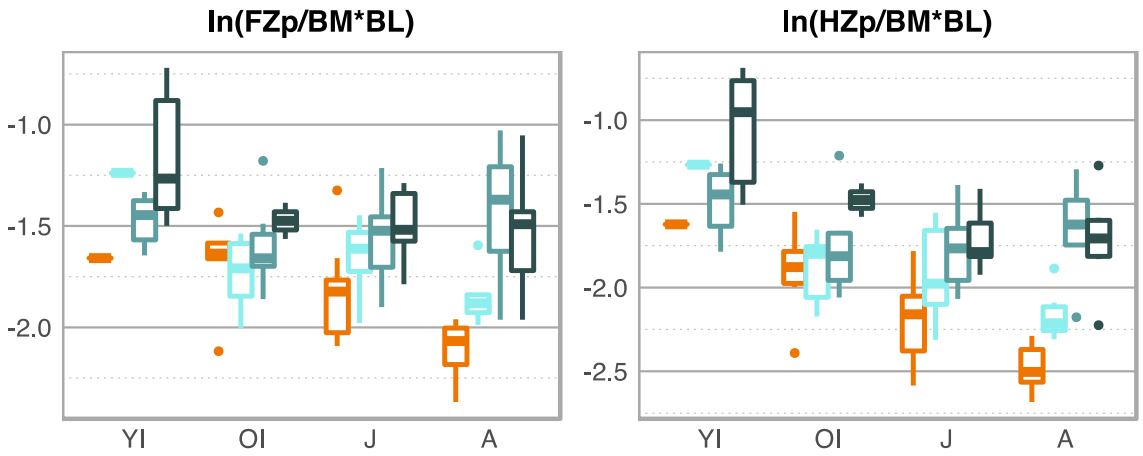

Figure 3.18 Box plots of scaled femoral and humeral Zp residuals in the four non-adult age groups (YI = young infant, OI = old infant, J = juvenile, and A = adolescent). Patterns are slightly different between the fore- and hind limb but are similar within other limb bones (not pictured). See Table 3.12 for significant post-hoc differences between taxa within each age group. Color key same as previous.

Bone Zx/Zy ratios show less change with age than the previously discussed variables and were also generally not different between taxa, with the exception of both the femur and humerus. Femoral shape ratios decline with age in all taxa, but again, bonobos appear to be shifted above other *Pan*, with *P. t. schweinfurthii* and *P. t. troglodytes* somewhat intermediate and *P. t. verus* lower (Figure 3.19). This pattern is essentially maintained in all age cohorts (Figure 3.20), with significant differences found between *P. t. verus* and the other two *P. troglodytes* subspecies in juveniles. The humerus shows much less directional change with age, but here, *P. t. verus* and *P. paniscus* tend to have higher values than the other two taxa, reaching statistical significance in comparisons of *P. t. verus* and *P. t. schweinfurthii* in juveniles (Figure 3.19, Figure 3.20, Table 3.12). No comparisons of shape are statistically significantly different between bonobos and any individual common chimpanzee subspecies (Table 3.12). Otherwise,

taxa appear to follow similar trajectories that appear to be primarily a function of circularity of adult cross-sectional shape (e.g., tibia vs. radius, Figure 3.19).

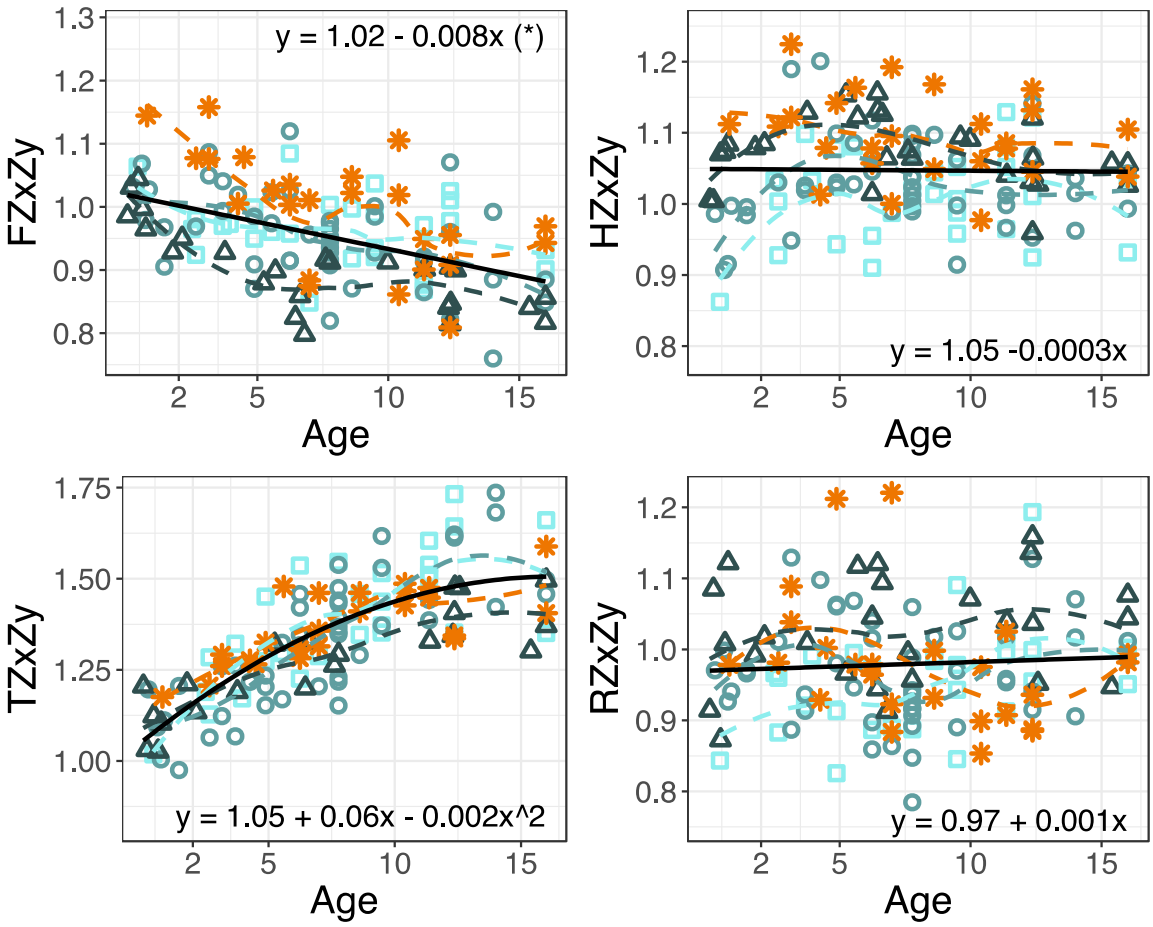

Figure 3.19 Growth in shape ratios (Zx/Zy) of the femur, humerus, tibia, and radius in P. paniscus *and* P. troglodytes *subspecies.* P. paniscus = *orange stars,* P. troglodytes = *blue (*P. t. schweinfurthii = *squares,* P. t. troglodytes = *circles,* P. t. verus = *triangles). Black line = pooled total sample equation, dashed lines = LOWESS fits for visualization of taxon-specific trends. * indicates significant difference between taxa in one or more age groups.*

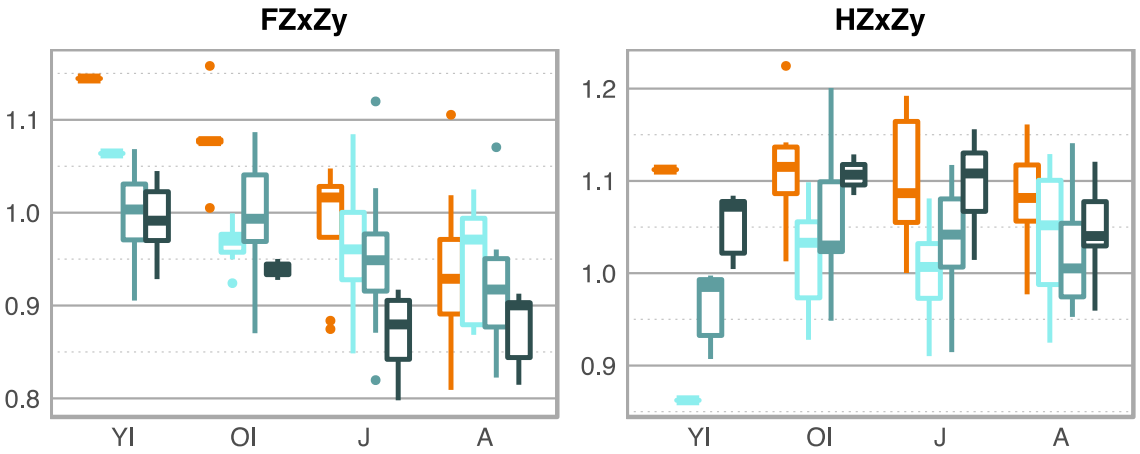

Figure 3.20 Box plots of femoral and humeral shape residuals in the four non-adult age groups (YI = young infant, OI = old infant, J = juvenile, and A = adolescent).). See Table 3.12 for significant post-hoc differences between taxa within each age group (including bones not pictured). Color key same as previous. See Table 3.12 for significant post-hoc differences.

3.2.2.4 Summary

As with lengths in the previous section, not all differences that were significant in adults are reflected during ontogeny, and vice versa, with some bone parameters different in subadults, but becoming more similar with age. Again, there was much more variation among *P. troglodytes* subspecies in cross-sectional parameters than in length proportions. Different aspects of cross-sectional geometry also did not track each other, i.e., they followed different ontogenetic trajectories even within the same bone.

Hind limb/forelimb strength ratios increase with age in all taxa. No significant differences are found among *P. troglodytes* subspecies, and ontogenetic trends in differences between *P. paniscus* and *P. troglodytes* depend on the ratio analyzed, with differences either increasing with age (femur/humerus), remaining constant with age (metatarsal/metacarpal), or showing a more complex pattern (tibia/radius). Intra-limb strength ratios showed less clear patterns of ontogenetic differences (and those that were significantly different between species as a whole were not always in subspecies separately). Metacarpal/humerus strength showed a fourth pattern of increasing similarity between taxa with age. Ulna/radius strength also differed between *P. t. verus* and both *P. paniscus* and *P. t. schweinfurthii* (the only intra-*P. troglodytes* subspecies difference found in cross-sectional strength ratios).

Scaled bone strengths tend to follow a fairly common pattern, with bonobos diverging downward from the three *P. troglodytes* subspecies with age. Based on comparisons between bonobos and *P. troglodytes* subspecies, it seems possible that this process may be accelerated in the forelimb bones, as both the humerus and radius reach

statistical significance in the juvenile age group, while all other bones are not significantly weaker in bonobos until adolescence. This would help to explain the trends in inter-limb cross-sectional strength ratios.

Lastly, shape ratios generally showed fewer taxonomic differences. Differences between bones in patterns of ontogenetic change seemed mostly to be due to variation in the final shape of the cross-section. All bones are more circular at birth, so those that are relatively round as adults showed less ontogenetic change than those that are less so. Here there were no differences between bonobos and common chimpanzees either as a group or as individual subspecies, although bonobo femora are noticeably less circular than those of *P. troglodytes* in infancy (Figure 3.20). There were, however, several differences within *P. troglodytes*, with *P. t. verus* having lower values for femoral shape and higher for humeral shape (both are less circular than those of the other taxa, although in the opposite direction). It is worth noting that, although statistical significance is not reached, *P. paniscus* is more similar to *P. t. verus* in humeral shape than it is to the other *P. troglodytes* subspecies, which is not true for femoral shape.

3.2.3 Comparison to behavioral data and Discussion

Based on Hypothesis 2, that bone cross-sectional strength ratios are more developmentally or behaviorally plastic, bone strength proportions and cross-sectional shape ratios (Zx/Zy) were predicted to be more consistent with behavioral variation than phylogenetic relationships. The data broadly support this prediction: in adults, there was only one instance (tibia/radius strength) in which bonobos differed from all three common chimpanzee subspecies in the same way, and there were also many instances in which the three subspecies differed from each other (in contrast to length proportions, in

which there were very few differences between *P. troglodytes* subspecies). This was also true during ontogeny, in which only two variables in one age group were different between bonobos and all three subspecies (Table 3.12).

In adults, the prediction that hind to forelimb strength should match relative amounts of hind limb versus forelimb loading behavior is largely borne out. According to these predictions, *P. t. verus* should have lower values than *P. paniscus* and *P. t. schweinfurthii*, in keeping with the former's higher frequencies of forelimb loading behavior both overall and within the subset of arboreal locomotor behavior. Differences between taxa are most pronounced in the tibia/radius ratio, and are only significantly different in femur/humerus ratio between *P. paniscus* and *P. t. troglodytes* and *P. t. verus* – although this also tracks behavioral data fairly well, as *P. t. schweinfurthii* from Gombe and Mahale are actually more similar to *P. paniscus* in overall frequencies of quadrupedalism than they are to *P. t. verus* (Figure 3.21; also see Chapter 1). Femoral shape also tracks differences in quadrupedalism, with the more quadrupedal taxa having more A-P strengthened femora (Figure 3.14). However, an alternative explanation, the relatively higher frequencies of leaping behaviors found by some earlier authors, cannot necessarily be ruled out. Ratios between elements within the same limb are generally more constant than those between bones in different limbs, except for within the forelimb: here, relative radius strength compared to the ulna is highest in *P. t. verus*, which is consistent with other findings from gorillas, in which more arboreal behavior was associated with higher radial strengths (Ruff et al., 2013).

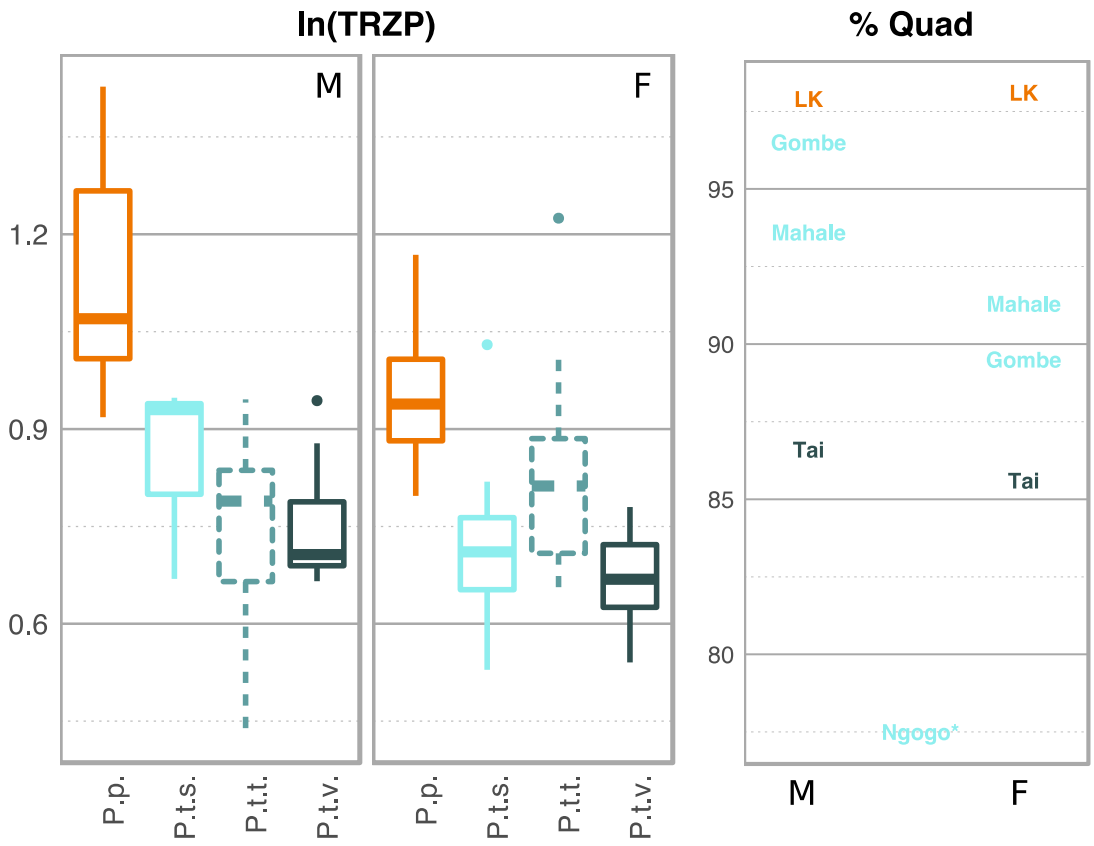

Figure 3.21 Tibia to radius strength and overall frequencies of quadrupedalism in P. paniscus *(orange),* P. t. schweinfurthii *(light blue),* P. t. troglodytes *(medium blue), and* P. t. verus *(dark blue). Dashed outline indicates morphological data without corresponding behavioral data, frequencies of quadrupedalism are separated by site (LK = Lui Kotale). *Ngogo data not reported for males and females separately.*

However, patterns of variation in cross-sectional strength ratios and shapes do not match entirely with predictions. It is difficult to determine why *P. t. schweinfurthii* would tend to have more A-P strengthened ulnae than other taxa, or why the relatively large behavioral differences between female *P. paniscus* and *P. t. schweinfurthii* are not matched by correspondingly large differences in femoral/humeral strength (Figure 3.12), while tibia/radius strength parallels behavioral differences quite well (Figure 3.21). Additionally, when *P. t. schweinfurthii* populations are compared separately, the picture

becomes more complex: the Ngogo chimpanzees are found to be substantially less quadrupedal than their conspecifics, even *P. t. verus*, which are generally considered to be the least quadrupedal subspecies (Figure 3.21). The Ngogo population may be an outlier, or the results of this study may indicate substantially broader behavioral diversity in *P. t. schweinfurthii* than previously recognized. Based on the currently available literature, both fore to hind limb cross-sectional strengths and femoral shape are most consistent with *P. t. schweinfurthii* being more quadrupedal and less suspensory than *P. t. verus*, not the opposite. However, the true extent of behavioral variability in this taxon is still not understood, so this interpretation should be taken with caution (as samples cover a broader range of localities than are sampled by behavioral studies) until more behavioral studies are available.

Hypothesis 2 also generated the prediction that fore- to hindlimb strength would decrease with age in all species/subspecies, following changes in behavior. Again, this is borne out by the data: all taxa decrease in fore/hindlimb strength ratios with age, concurrent with age-related decreases in forelimb-dominated behaviors such as climbing and suspension (Figure 3.22; also see Chapter 1), and very unlike age patterns in length ratios. Also, infants tend to be more similar in these proportions, with differences increasing with time.

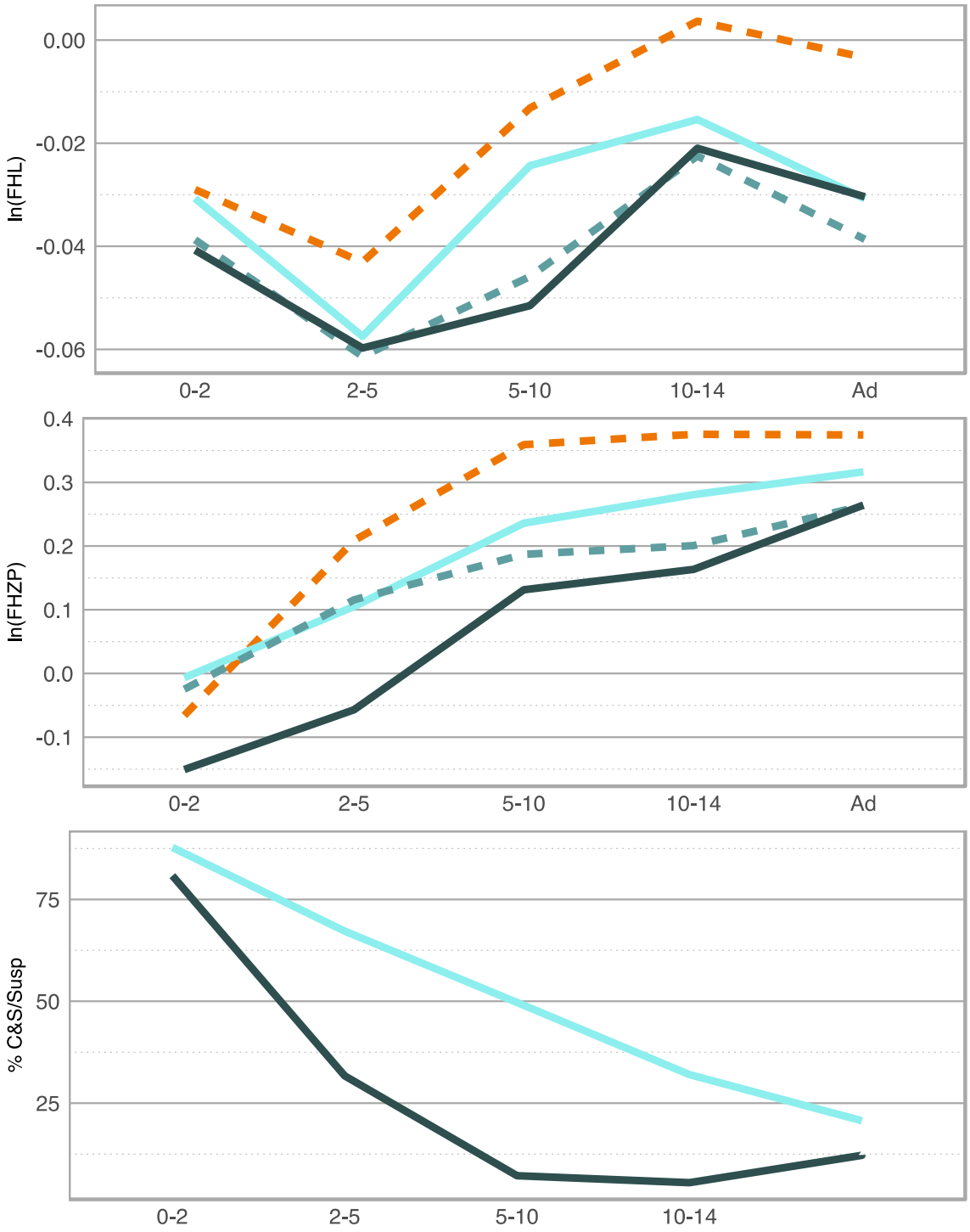

Figure 3.22 Mean values in each age/taxon group for femur/humerus length (top), strength (middle), and total percentage of climbing and suspensory behavior (bottom) for P. paniscus *(orange),* P. t. schweinfurthii *(light blue),* P. t. troglodytes *(medium blue), and* P. t. verus *(dark blue). Dashed lines = no ontogenetic behavioral data.*

The overall trends of cross-sectional shape away from circularity are consistent both with increasing quadrupedalism and with general growth patterns necessary to attain adult cross-sectional shape from a bone that is circular at birth. Unlike in adults, shape ratios show few differences during ontogeny, except in the femur and humerus. Bonobo infants have noticeably more A-P strengthened femora and humeri. *P. t. verus* is more similar to bonobos in humeral shape, but has the *lowest* mean femoral strength ratios in all age groups (Figure 3.19). These are difficult to reconcile with behavioral patterns, as based on behavior *P. t. verus* should have more circular bones at all ages. It may be that bone shapes are less informative of small-scale behavioral variation (Carlson et al., 2006), or that the types of arboreal behaviors practiced by *P. t. verus* include more stereotypical loading than those practiced by other *Pan*.

In addition to these more general patterns, there is some suggestion that femur/humerus strength may track differences in rates of change between different taxa. *P. t. verus* seem to show a more drastic decrease in forelimb-dominated behaviors during infancy and also have slightly larger increases in forelimb/hindlimb strength during this time (from mean values of -0.151 in young infants to 0.131 in juveniles, versus -0.001 to 0.24 over the same age classes in *P.t. schweinfurthii*). If this is true, then patterns of changes in cross-sectional properties in the two taxa with no ontogenetic behavioral data suggest that *P. t. troglodytes* are likely similar to *P. t. schweinfurthii* in patterns of ontogenetic behavioral change, but that bonobos may show an even more precipitous decrease in climbing and/or suspension over this time period. However, not all fore- hind limb ratios show this same seeming relationship with rates of behavioral change – mean differences between taxa in tibia/radius strength are essentially constant through all non-

adult age periods (Figure 3.23). In adults, tibia/radius strength more strongly discriminated between subspecies than femur/humerus strength. This may indicate that behavior has different impacts on cross-sectional strength at different points along the limb (metatarsal/metacarpal strength was similar in bonobos and all subspecies both in adults and across ontogeny, see Discussion).

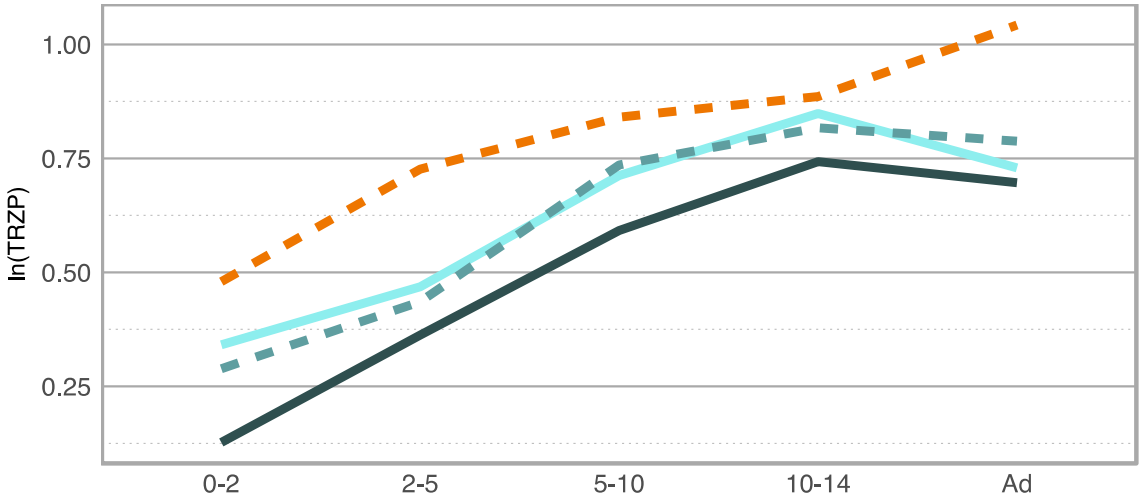

Figure 3.23 Mean values for tibia/radius strength in P. paniscus *(orange),* P. t. schweinfurthii *(light blue),* P. t. troglodytes *(medium blue), and* P. t. verus *(dark blue). Dashed lines = no ontogenetic behavioral data.*

Metacarpal/humerus strength also showed some ontogenetic differences. Compared to *P. troglodytes,* bonobos have higher values in infancy and become progressively similar with age (despite complete overlap in metacarpal/humerus length). In the absence of both ontogenetic behavioral data for *P. paniscus* and any significant differences between adults, it is difficult to interpret these patterns. However, it seems likely that they may be due to differences in hand postures throughout life.

While patterns of change *within* species and subspecies are consistent with interpretations based on behavioral data, differences between subspecies are not necessarily. *P. t. verus* have the lowest hind limb/forelimb strength ratios in all age

categories. This is the reverse of what would be expected from ontogenetic behavioral data, which show them as being relatively more quadrupedal/less forelimb dominated than *P. t. schweinfurthii* during ontogeny (although adults show the opposite pattern of differences). Again, however, this is impacted by the differences found between Ngogo and other populations of *P. t. schweinfurthii*, as ontogenetic *P. t. schweinfurthii* data are based solely on the Ngogo population and so may be reflective of the same tendency towards high frequencies of climbing and suspension rather than quadrupedalism. As with adults, it is still unclear whether this population is an outlier from broader *P. t. schweinfurthii* behavioral trends, but cross-sectional strength ratios for this taxon are more consistent with lower frequencies of forelimb dominated behaviors than *P. t. verus*. Further ontogenetic studies of other *P. t. schweinfurthii* populations are necessary to clarify these issues.

Overall, these results are consistent with the hypothesis that bone cross-sectional strengths are reflective of behavioral diversity. The fact that differences between *P. troglodytes* subspecies were found suggests that future studies of cross-sectional geometry in the genus *Pan* should control for subspecies, if possible. Additionally, because adult bonobos do not resemble immature common chimpanzees in limb strength ratios, results are less consistent with the idea that bonobos are "locomotor paedomorphs" and more consistent with recent behavioral studies suggesting that locomotor repertoires may be more similar. Ontogenetic locomotor data for bonobo populations are necessary to further test this prediction.

3.3 JOINT SIZES AND JOINT SIZE RATIOS

This section covers measurements of joint sizes, both absolute and relative to one another, for the long bones covered in the study. Like bone lengths, joint dimensions are not measurable throughout the entire ontogenetic period, as the joints of young individuals are not sufficiently developed to be comparable to adult morphology and, prior to fusion, are often missing in skeletal collections. However, unlike metaphyseal and total bone lengths, joint breadths and their underlying metaphyseal breadths, where both are measurable on the same specimens, are not as strongly correlated across different age groups (data not shown), perhaps because of more dramatic ontogenetic change in the shape of the epiphysis. Because of this, no attempt was made to construct conversion equations like those used for limb bone lengths, and consequently analyses in this section are slightly different than those in the previous two sections.

Variables analyzed are listed in Table 3.13 and Table 3.14. Five joint measurements and underlying metaphyseal breadths are included in both adult and ontogenetic analyses. Femoral and humeral head breadths are included in adult analyses, because they are some of the most frequently analyzed joint surfaces and are functionally informative (see Introduction). No corresponding metaphyseal breadths were measured, so these are not included in ontogenetic analyses. Raw measurements were used to construct a number of inter- and intra-limb ratios, which were natural logged in all analyses for methodological considerations. For adults, raw joint measurements were also logged for analyses to allow more variables to meet normality and equality of variance assumptions. For ontogenetic analyses, which make no such assumptions, results from

logged and unlogged variables were similar, so no log transformation of raw variables was undertaken.

Analyses for adults proceeded as in previous sections. However, because metaphyseal dimensions are not measurable on older specimens, and joint dimensions are not measurable on younger specimens, ontogenetic data do not cover the full age span and thus cannot be fit by a single polynomial as in limb lengths and strengths. Therefore, instead of polynomial residuals, raw values were grouped by age bin, using metaphyseal breadths for young and old infants and juveniles and articular breadths for adolescents. (Although some juveniles had measurable articular breadths and some adolescents measurable metaphyseal breadths, this configuration maximizes sample sizes in each group). Wilcoxon rank-sum tests, either single or pairwise between subspecies with Bonferroni correction applied, were then used to test for taxon differences within the Old Infant, Juveniles, and Adolescent age bins (although data scatters are depicted visually for all four groups, see Methods).

Table 3.13 Joint size variables

Variable	Abbreviation
Raw variables	
Femoral head SI breadth	FHSI
Distal femoral ML breadth	FDML
Proximal tibial ML breadth	TPML
Humeral head SI breadth	HHSI
Distal humeral ML breadth	HDML
Proximal radial ML breadth	RHML
Proximal ulnar ML breadth	UPML
Derived variables	
Femoral head/Humeral head breadth*	FH/HH
Distal femoral/Distal humeral breadth	FD/HD
Proximal tibial/Proximal radial breadth	TP/RH
Proximal tibial/Distal femoral breadth	TP/FD
Proximal radial/Distal humeral breadth	RH/HD
Proximal ulnar/Distal humeral breadth	UP/HD
Proximal ulnar/Proximal radial breadth	UP/RH
Distal femoral/Femoral head breadth*	FD/FH
Distal humeral/Humeral head breadth*	HD/HH

Table 3.14 Metaphyseal size variables

Variable	Abbreviation
Raw variables	
Distal femoral metaphyseal ML breadth	FDMLm
Proximal tibial metaphyseal ML breadth	TPMLm
Distal humeral metaphyseal ML breadth	HDMLm
Proximal radial metaphyseal ML breadth	RPMLm
Derived variables	
Distal femoral/Distal humeral metaphyseal breadth	FDm/HDm
Proximal tibial/Proximal radial metaphyseal breadth	TPm/RHm
Proximal tibial/Distal femoral metaphyseal breadth	TPm/FDm
Proximal radial/Distal humeral metaphyseal breadth	RHm/HDm
Proximal ulnar/Distal humeral metaphyseal breadth**	UPm/HDm
Proximal ulnar/Proximal radial metaphyseal breadth**	UPm/RHm

* Ratios not included in ontogenetic analyses

** Proximal ulnar articular breadth is measurable on all individuals and is thus used in these ratios.

3.**3.1 Adults**

Summary statistics (means and standard deviations) for adult lengths and length ratios, by sex, can be found in Table 3.15 and Table 3.16.

3.3.1.1 Species-level analyses

Sex differences within each species were tested with two sample t-tests with unequal variance in normally distributed variables and Mann-Whitney U tests in non-normally distributed variables. Significance levels were Bonferroni-corrected ($\alpha < .05/2$). Joints are significantly larger in males than in females in *P. troglodytes*, but are not significantly different between sexes in *P. paniscus*. Joint ratios are also similar between sexes in both species, except for HD/HH, which is larger in males in *P. troglodytes* (Table 3.15). Accordingly, sexes were analyzed separately for both this ratio and for raw joint dimensions, and were pooled for all other measurements.

Figure 3.24 shows box and whisker plots for joints and joint ratios. As with analyses of sex differences, species differences were tested with two sample t-tests with unequal variance or Mann-Whitney U tests (see Table 3.15). For sex-separated comparisons, significance levels were Bonferroni adjusted ($\alpha < .05/2$).

All joints tend to be absolutely larger in *P. troglodytes* than in *P. paniscus* in both sexes. These differences reach significance in males for all joints, but only for the humeral head, radial head, and proximal ulna in females (Figure 3.24).

Table 3.15 Summary statistics for and sex differences in joints and joint ratios in adults (species)

	P. paniscus						***P. troglodytes***					
	Male			**Female**			**Male**			**Female**		
Variable	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**
FDSI	9	31.09	1.27	10	30.74	1.53	31	**33.45**	1.80	41	**31.70**	1.92
FDML	9	51.22	3.08	10	49.19	2.82	31	**55.11**	3.99	41	**51.68**	3.58
TPML	9	55.34	2.44	10	53.39	1.86	30	**59.26**	3.42	42	**55.28**	2.89
HDSI	9	35.17	1.81	10	34.25	1.96	30	**39.99**	2.85	42	**37.72**	2.32
HDML	9	41.01	2.17	10	38.59	2.69	30	**44.13**	2.73	41	**40.25**	2.71
RHML	9	22.11	0.97	9	21.33	1.58	30	**25.04**	1.74	43	**22.96**	1.70
UPML	9	22.39	1.53	10	21.05	1.90	29	**24.99**	2.05	42	**22.82**	1.87
FH/HH	9	-0.123	0.042	10	-0.108	0.040	30	-0.176	0.050	40	-0.174	0.041
FD/HD	9	0.222	0.037	10	0.243	0.047	30	0.224	0.051	40	0.249	0.061
TP/RH*	9	0.917	0.046	9	0.899	0.041	29	0.863	0.054	40	0.877	0.062
TP/FD	9	0.078	0.035	9	0.076	0.033	30	0.074	0.049	39	0.065	0.043
RH/HD	9	-0.617	0.032	10	-0.594	0.056	29	-0.571	0.039	42	-0.562	0.065
UP/HD	9	-0.606	0.089	10	-0.608	0.055	28	-0.573	0.061	41	-0.568	0.065
UP/RH	9	0.011	0.066	10	-0.014	0.088	29	-0.006	0.060	42	-0.007	0.075
FD/FH	9	0.498	0.055	10	0.470	0.053	31	0.498	0.054	40	0.489	0.065
HD/HH	9	0.154	0.071	10	0.119	0.060	30	**0.099**	0.048	42	**0.065**	0.052

Bold values are significantly different between males and females within species
** Not normally distributed; see text for details of analysis*

Joint ratios, however, tend to be more similar between the two taxa, with some exceptions. The femoral head is relatively larger than the humeral head in *P. paniscus* than in *P. troglodytes* (FH/HH), and the tibial plateau is also relatively larger than the radial head (TP/RH; Figure 3.24). There are also several differences within the forelimb joints. *P. paniscus* have a significantly relatively larger distal humerus compared to the radial head. This measurement tends to be large relative to the proximal ulna as well (although the difference does not reach significance), so the two species are virtually identical in radial to ulnar articular surface proportions. The distal humerus in bonobos is also relatively large compared to the humeral head, although this is significant only in females.

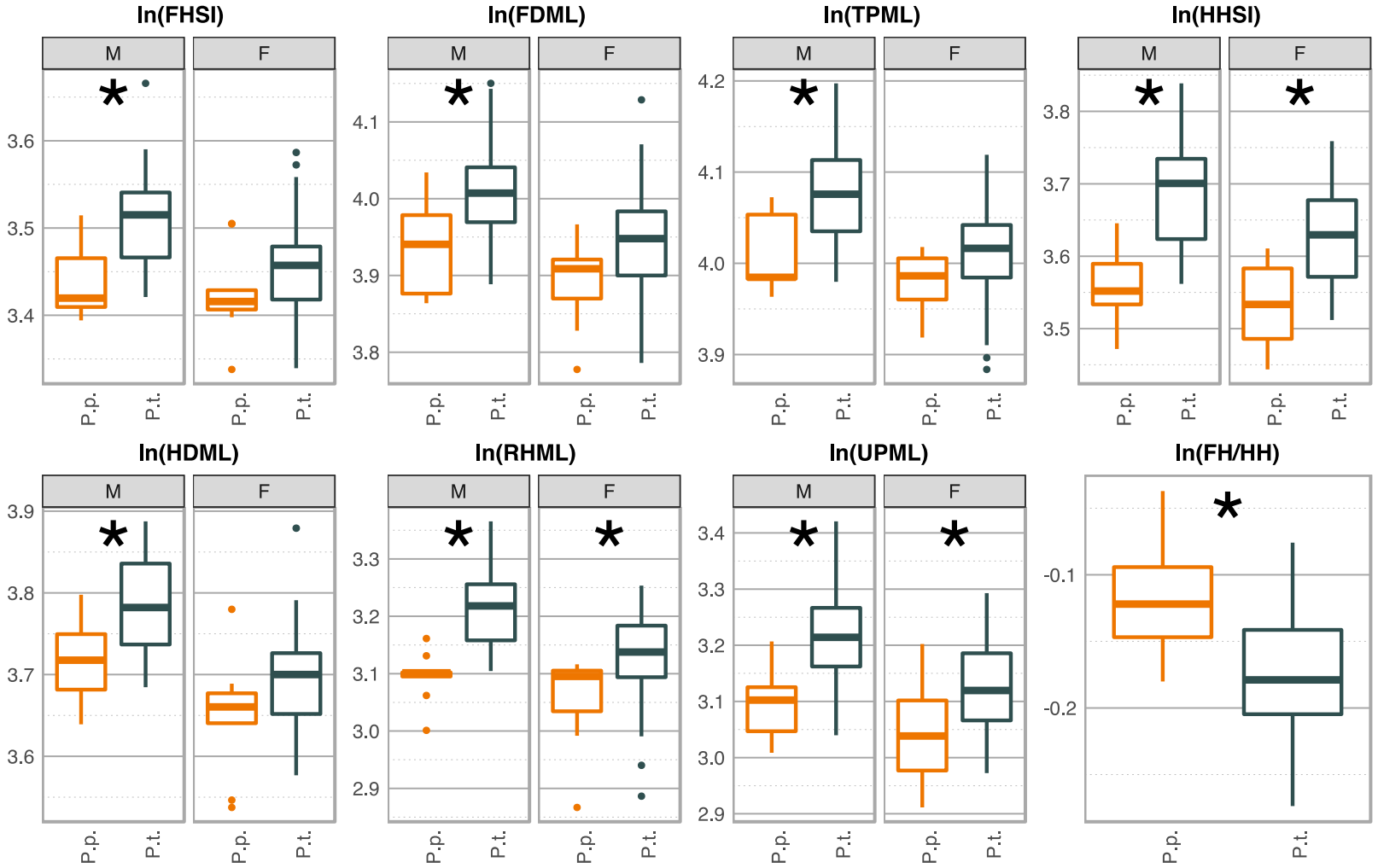

Figure 3.24 Boxplots of joints and joint ratios in P. paniscus *and* P. troglodytes *males and females. Significant differences between taxa are indicated with large black asterisks. P.p.* = Pan paniscus*; P.t.* = P. troglodytes.

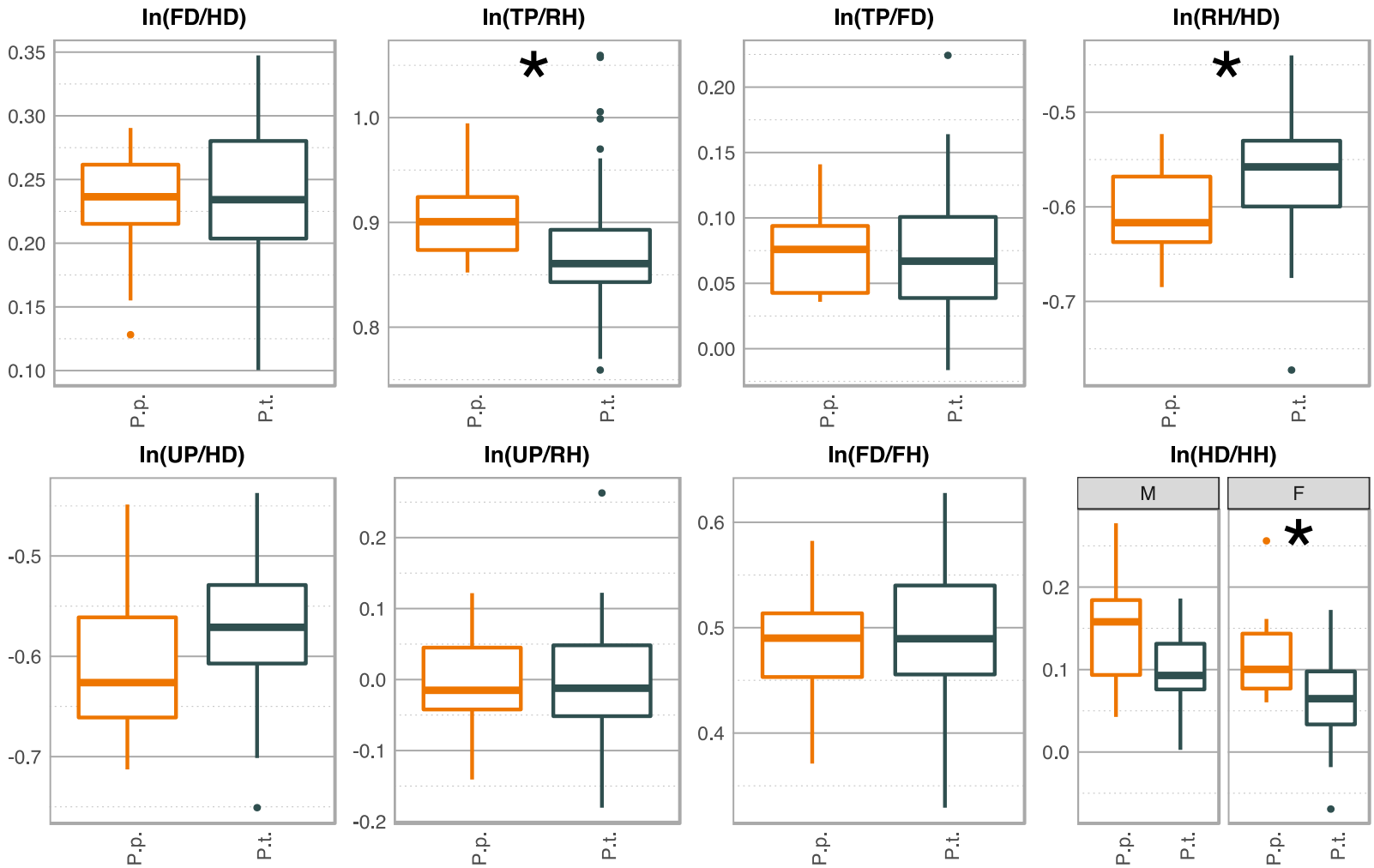

Figure 3.24, cont'd.

3.3.1.2 Subspecies-level analyses

Again, sex differences were first tested with two sample t-tests with unequal variance or Mann-Whitney U tests with Bonferroni-corrected significance levels, with family-wise error rate of .0167 (reported in Table 3.16; bonobos were again not included in this analysis as they have been previously analyzed). Results are similar to species-level analyses in that sexes did not differ in any joint size ratios, but raw joint dimensions do not reach statistical significance between sexes in all three subspecies (although males were significantly larger than females for all joint dimensions in *P. t. troglodytes*, Table 3.15). Thus, sexes were pooled for analyses of ratios and kept separate for raw measurements.

Figure 3.25 shows boxplots of joints and joint ratios. As in previous sections, these were tested with one-way ANOVA (or with Kruskal-Wallis tests if variables were not normally distributed or had unequal variance, see Table 3.16), with Games-Howell tests used to test for pairwise differences between subspecies. All p values were Bonferroni corrected to a family-wise significance level of .05.

Results for joint measurements are similar to those at the species level in that there are significant effects of taxon in males for all joints measured, and in females for the forelimb joints (including HDML, which was not significantly different in females at the species level). However, there is additional variation within *P. troglodytes* subspecies such that not all differ from bonobos. In males, all joints measured are larger in *P. t. troglodytes* than in *P. paniscus*, and there are similar differences between *P. paniscus* and *P. t. schweinfurthii* in the distal humerus and between *P. t. troglodytes* and *P. t. schweinfurthii* in the proximal tibia (Figure 3.25). Differences in females are less

pronounced and are somewhat more likely to be between *P. troglodytes* subspecies: female *P. paniscus* have smaller humeral heads than female *P. t. verus* and *P. t. troglodytes* and smaller radial heads than *P. t. verus*, but differences in the distal humerus and proximal radius are observed between subspecies of *P. troglodytes* rather than between *P. troglodytes* subspecies and *P. paniscus*.

In joint ratios, again, proportions that are different between bonobos and common chimpanzees as a whole also tend to differ between bonobos and common chimpanzee subspecies, but all subspecies are not always significantly different (Figure 3.25). One exception to this is femoral head/humeral head (FH/HH), which differs between bonobos and all three subspecies. Tibial plateau/radial head breadth follows a different pattern, decreasing from bonobos and *P. t. schweinfurthii* to *P. troglodytes* to *P. t. verus,* but only differing significantly between the first and the last (Figure 3.25). The other exception is distal humerus/proximal humerus ratios, which are larger in bonobos than in all *P. troglodytes*. Other major differences involve *P. t. verus*, which have significantly smaller humeral heads relative to both radial and ulnar heads than all other taxa.

Table 3.16 Summary statistics for and sex differences in joints and joint ratios in adults (subspecies)

	P. t. schwein.						***P. t. trog.***						***P. t. verus***					
	Male			**Female**			**Male**			**Female**			**Male**			**Female**		
Variable	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**
FDSI*	3	33.24	0.73	8	31.26	2.26	18	**34.03**	2.03	18	**31.97**	2.15	11	32.48	1.08	10	31.62	1.46
FDML	3	52.33	3.31	8	49.25	3.03	18	**56.55**	3.84	19	**52.52**	3.81	11	53.36	3.56	10	51.92	3.11
TPML	2	40.01	2.80	7	36.46	2.36	18	**40.83**	2.70	19	**38.47**	2.40	11	38.30	2.69	9	37.45	1.96
HDSI	3	44.13	0.66	8	38.01	2.22	18	**45.04**	2.58	19	**41.59**	2.70	11	42.33	2.70	9	39.76	2.01
HDML	3	**54.84**	0.93	8	**53.27**	2.10	18	**60.24**	3.17	19	**55.67**	3.54	11	58.37	3.40	10	55.72	1.83
RHML*	3	24.57	1.53	8	21.34	1.33	18	**25.32**	1.69	19	**23.07**	1.94	11	24.63	1.95	9	23.63	0.95
UPML	2	**25.40**	0.70	8	**21.36**	1.91	18	**24.93**	2.01	19	**22.91**	1.56	11	25.02	2.44	9	23.49	1.89
FH/HH	3	-0.184	0.049	8	-0.154	0.032	18	-0.182	0.050	18	-0.183	0.048	11	-0.161	0.054	9	-0.172	0.032
FD/HD	3	0.169	0.049	8	0.259	0.056	18	0.227	0.045	19	0.233	0.070	11	0.237	0.056	9	0.267	0.046
TP/RH*	2	0.832	0.041	7	0.918	0.051	18	0.867	0.062	19	0.882	0.077	11	0.860	0.039	9	0.849	0.015
TP/FD	2	0.452	0.047	7	0.455	0.090	18	0.507	0.052	19	0.497	0.065	11	0.495	0.056	10	0.498	0.043
RH/HD	3	0.100	0.058	8	0.042	0.036	18	0.099	0.047	19	0.078	0.053	11	0.101	0.054	9	0.060	0.057
UP/HD	2	0.078	0.037	8	0.084	0.050	18	0.064	0.051	19	0.059	0.046	11	0.090	0.048	9	0.065	0.033
UP/RH	2	-0.587	0.048	8	-0.577	0.059	18	-0.576	0.040	19	-0.591	0.065	11	-0.552	0.031	9	-0.518	0.041
FD/FH	3	-0.561	0.022	8	-0.578	0.041	18	-0.593	0.058	18	-0.597	0.053	11	-0.530	0.057	10	-0.524	0.070
HD/HH	3	0.000	0.002	8	-0.001	0.077	18	-0.017	0.068	19	-0.006	0.085	11	0.014	0.043	9	-0.013	0.063

Bold values are significantly different between males and females within subspecies

** Not normally distributed and/or unequal variance; see text for details of analysis*

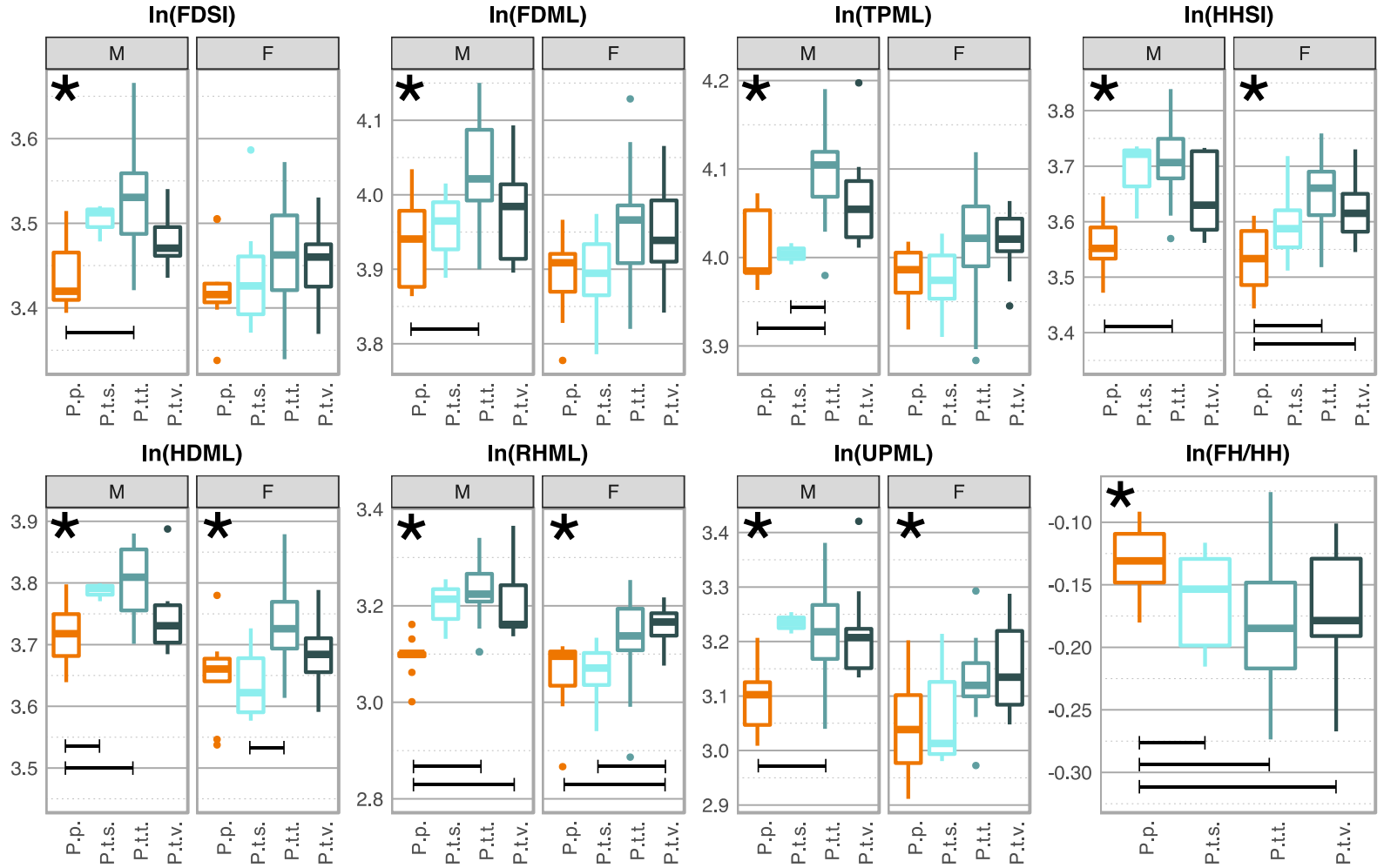

Figure 3.25 Boxplots of joint measurements in P. paniscus *(P.p.),* P. t. schweinfurthii *(P.t.s.),* P. t. troglodytes *(P.t.t.), and* P. t. verus *(P.t.v.). Significant overall differences between taxa (within sexes) are indicated with large black asterisks; significant post-hoc comparisons, where present, are indicated with brackets.*

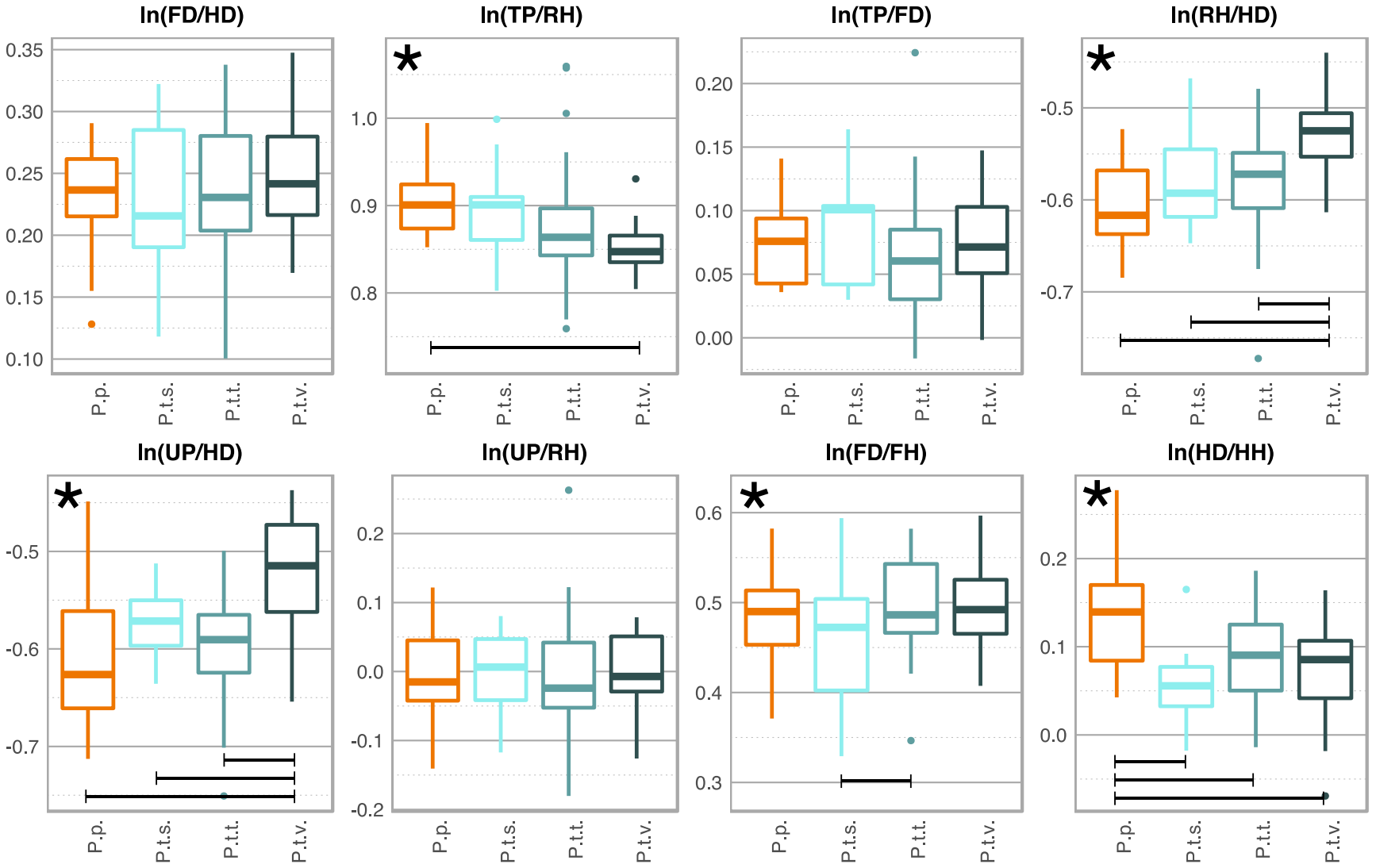

Figure 3.25, cont'd.

3.3.1.3 Summary

In summary, adult *P. troglodytes* show sexual dimorphism in all joint sizes, while adult *P. paniscus* do not (probably related to overall greater levels of sexual dimorphism in body size in the former). Within sexes, *P. troglodytes* tend to have larger joints than *P. paniscus*, but while this difference is significant in males for all joints, it is only significant in the forelimb joints in females (which may also relate to the lack of sexual dimorphism in *P. paniscus* discussed in the Introduction). There is some variation within *P. troglodytes* such that not all subspecies differ significantly from *P. paniscus*: in males, most differences were found between *P. t. troglodytes* and *P. paniscus*, with the other two subspecies intermediate, while in females, more differences were found between *P. t. verus* and the other taxa considered.

Joint size ratios, on the other hand, are somewhat more similar both between sexes and across taxa. The humeral head is relatively small relative to both the femoral head and the distal humerus in *P. paniscus* compared to both *P. troglodytes* as a whole and each individual subspecies separately, but other joint size ratios that differed at the species level were not consistently different between bonobos and all three subspecies. No species-level differences were found in the relative sizes of the proximal radius and ulna, but between subspecies, *P. t. verus* have significantly smaller humeral heads relative to both radial and ulnar heads than all other taxa.

3.3.2 Ontogenetic

3.3.2.1 Species-level analyses

Wilcox rank-sum tests were used to test whether bonobos and common chimpanzees differed from each other in absolute and metaphyseal/joint ratios. Adult differences were tested in the previous section, so this section covers non-adult age cohorts only.

Table 3.17 contains species means and standard deviations in each age group, along with statistical significance of differences between species (epiphyseal breadths for adolescents, metaphyseal breadths for other age groups).

There are very few significant differences overall between bonobos and common chimpanzees within age groups, although in absolute measurements, as in adults, bonobos tend to have somewhat smaller joints even in the 2-5 year age group. (In Young Infants, values tend to be more similar, but sample sizes are extremely small and only include one bonobo). While the knee joints never reach statistical significance, either or both the proximal radius and distal humerus are significantly larger in common chimpanzees during later infancy, juvenile, and adolescent periods (Table 3.17). In joint and metaphyseal ratios, again, there are very few significant differences or overall trends, especially in intra-limb ratios. Bonobos do tend to have somewhat higher mean values for inter-limb ratios, but these only reach significance in adolescents

Table 3.17 Mean and (SD) of joint/metaphyseal variables within each species/age group

	Young Inf. (0-2y)				Old Inf. (2-5y)			
	P. pan.		*P. trog.*		*P. pan.*		*P. trog.*	
Variable	*n*	*mean(SD)*	*n*	*mean(SD)*	*n*	*mean(SD)*	*n*	*mean(SD)*
FDML	1	24.36(NA)	14	23.50(4.10)	4	29.11(2.02)	17	32.53(3.59)
TPML	1	18.77(NA)	14	18.56(3.59)	4	23.47(1.28)	16	26.09(3.35)
HDML	1	25.36(NA)	14	25.03(4.19)	4	**28.48(0.18)**	18	**32.19(3.06)**
RHML	1	8.72(NA)	14	9.10(1.36)	3	10.34(0.27)	17	11.64(1.01)
UPML	1	7.98(NA)	14	7.71(1.57)	4	10.05(0.20)	17	11.00(1.55)
FD/HD	1	-0.040(NA)	14	-0.064(0.053)	2	0.026(0.029)	17	0.004(0.064)
TP/RH	1	0.767(NA)	14	0.704(0.121)	3	0.800(0.029)	16	0.808(0.108)
TP/FD	1	-0.261(NA)	14	-0.241(0.052)	2	-0.225(0.058)	16	-0.214(0.045)
RH/HD	1	-1.068(NA)	14	-1.008(0.072)	3	-1.013(0.022)	17	-1.022(0.064)
UP/HD	1	-1.156(NA)	14	-1.179(0.127)	4	-1.042(0.025)	17	-1.084(0.085)
UP/RH	1	-0.089(NA)	14	-0.171(0.140)	3	-0.025(0.047)	17	-0.063(0.105)
	Juv. (5-10y)				**Adol. (10-14y)***			
FDML	5	39.55(3.03)	33	40.92(3.50)	8	46.40(3.59)	18	49.97(4.63)
TPML	6	32.25(3.32)	30	34.54(3.04)	8	37.41(3.00)	19	40.87(3.03)
HDML	6	**36.93(2.42)**	36	**42.33(5.03)**	7	51.23(2.74)	16	52.99(3.33)
RHML	6	**13.04(0.97)**	35	**14.88(1.69)**	8	**20.59(1.19)**	16	**22.83(1.96)**
UPML	8	14.01(2.38)	41	15.43(2.26)	8	20.61(2.36)	18	22.55(2.12)
FD/HD	4	0.080(0.093)	32	-0.032(0.080)	8	0.216(0.043)	18	0.202(0.059)
TP/RH	5	0.907(0.038)	27	0.850(0.071)	7	**0.908(0.037)**	13	**0.846(0.037)**
TP/FD	5	-0.200(0.058)	30	-0.174(0.054)	7	0.096(0.039)	16	0.053(0.047)
RH/HD	6	-1.041(0.081)	34	-1.046(0.065)	8	-0.596(0.052)	16	-0.584(0.063)
UP/HD	6	-1.035(0.132)	34	-1.032(0.068)	8	-0.599(0.069)	18	-0.602(0.071)
UP/RH	6	0.006(0.103)	34	0.019(0.099)	8	-0.003(0.099)	15	-0.018(0.075)

** All measurements metaphyseal breadths except for adolescents*
Bold values significantly different between species at family-wise alpha of .05

3.3.2.2 Subspecies-level analyses

Pairwise Wilcox rank-sum tests were used to test for differences between bonobos and the three common chimpanzee subspecies, with a family-wise alpha of .05. Figure 3.26 shows box plots for raw epiphyseal and metaphyseal measurements in each age group, and Figure 3.27 shows natural logged ratios of these measurements. Significant differences within each age group are noted in Table 3.18. Summary statistics for each age/subspecies group are found in the Appendix.

As expected, metaphyseal measurements increase with age in all taxa, showing little to no overlap in values between consecutive age groups. There is less change between adolescents and adults, which show substantial overlap in values (unsurprisingly, as epiphyses are largely formed by adolescence; Figure 3.26). There are no significant differences between *P. troglodytes* subspecies in raw joint measurements in any age group, although there is variation within them. This variation is especially noticeable in the youngest specimens, which may be due to either to greater variability overall at this time or to measurement error. Bonobos tend to have smaller joint and metaphyseal surfaces than *P. troglodytes*, and do differ from individual *P. troglodytes* subspecies in some forelimb joint dimensions, but not in the hind limb. The distal humerus is significantly narrower in bonobos than *P. troglodytes* in old infants, and than both *P. t. troglodytes* and *P. t. verus* in juveniles. (This trend continues through adolescence but is not statistically significant). The proximal radius also shows this trend, reaching significance in comparisons of bonobos and *P. t. verus* in juveniles. There is general similarity in patterns of differences in epiphyseal and metaphyseal dimensions.

Table 3.18 Significant differences between taxa within age groups in joint and metaphyseal measurements and ratios

	Significant differences*		
Variable	**Old inf**	**Juv**	**Adol**
Distal humerus	*P.p./P.t.t.*	*P.p./P.t.t. & P.t.v.*	
Proximal radius		*P.p./P.t.v.*	
Dist. fem./Dist. hum.		*P.t.t./P.t.v.*	
Prox. tib./Prox. rad.			*P.p./P.t.t.*

**P. p. = P. paniscus; P. t. s. = P. t. schweinfurthii,P. t. t. = P. t. troglodytes, P. t. v. = P. t. verus*

In metaphyseal and joint ratios (Figure 3.27), there are both much less pronounced differences between age groups and fewer significant differences between

taxa within these groups, with substantial overlap between all taxa. Again, there is substantial variation within *P. troglodytes* in the youngest age groups, but the patterning of this variation does not appear to follow clear taxonomic lines. For example, in the distal femur/distal humerus, *P. t. verus* have substantially lower values, reaching significance in comparisons with *P. t. troglodytes* in old infants. In the proximal tibia/proximal radius ratio, both *P. t. verus* and *P. t. schweinfurthii* young infants have the lowest values, and in adolescents, *P. t. troglodytes* are significantly lower than *P. paniscus*. There is even more overlap in within-limb comparisons, rendering interpretations difficult.

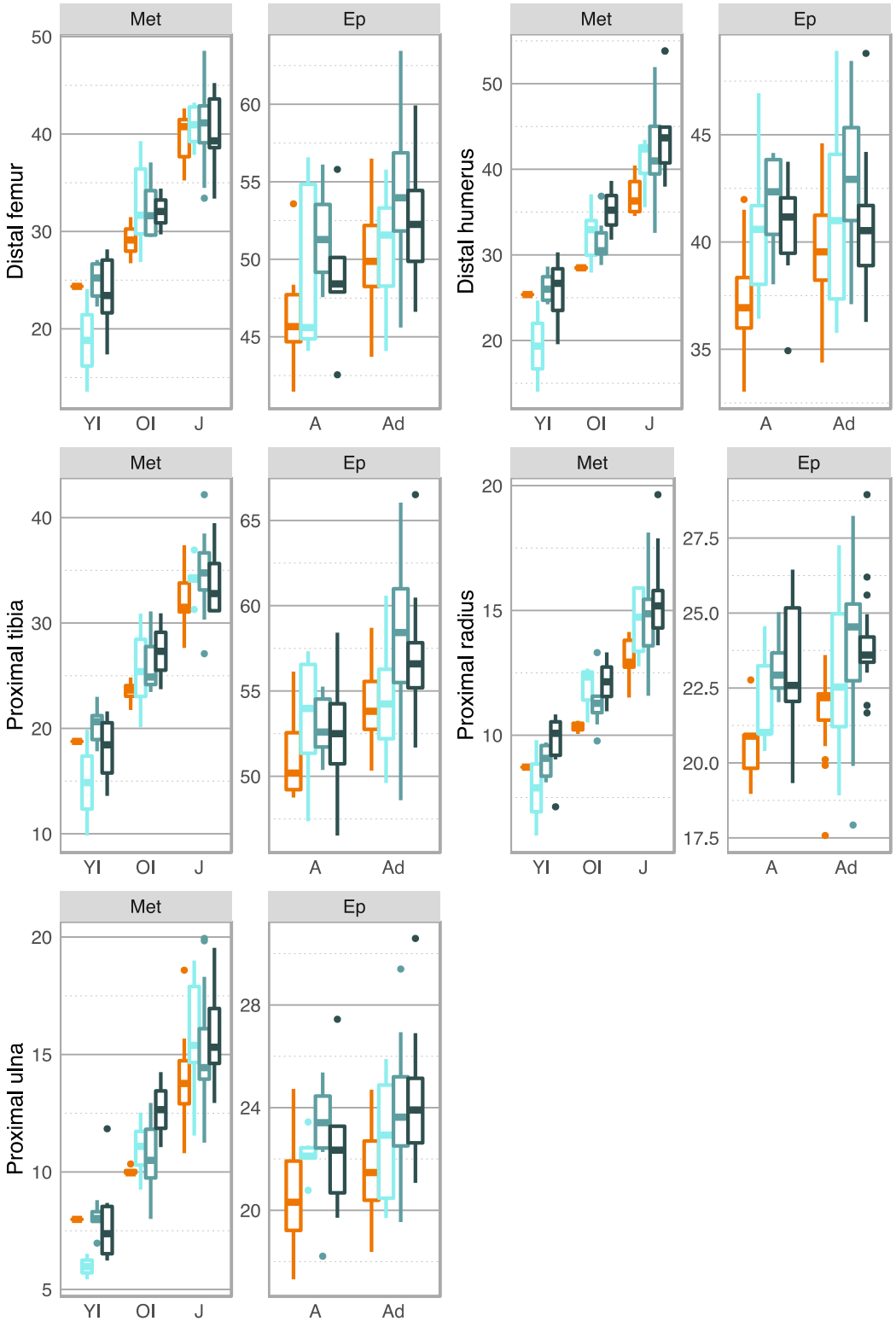

Figure 3.26 Joint (Ep) and metaphyseal (Met) measurements within each age group for P. paniscus *(Orange),* P. t. schweinfurthii *(light blue),* P. t. troglodytes *(medium blue), and* P. t. verus *(dark blue). See Table 3.18 for significant differences.*

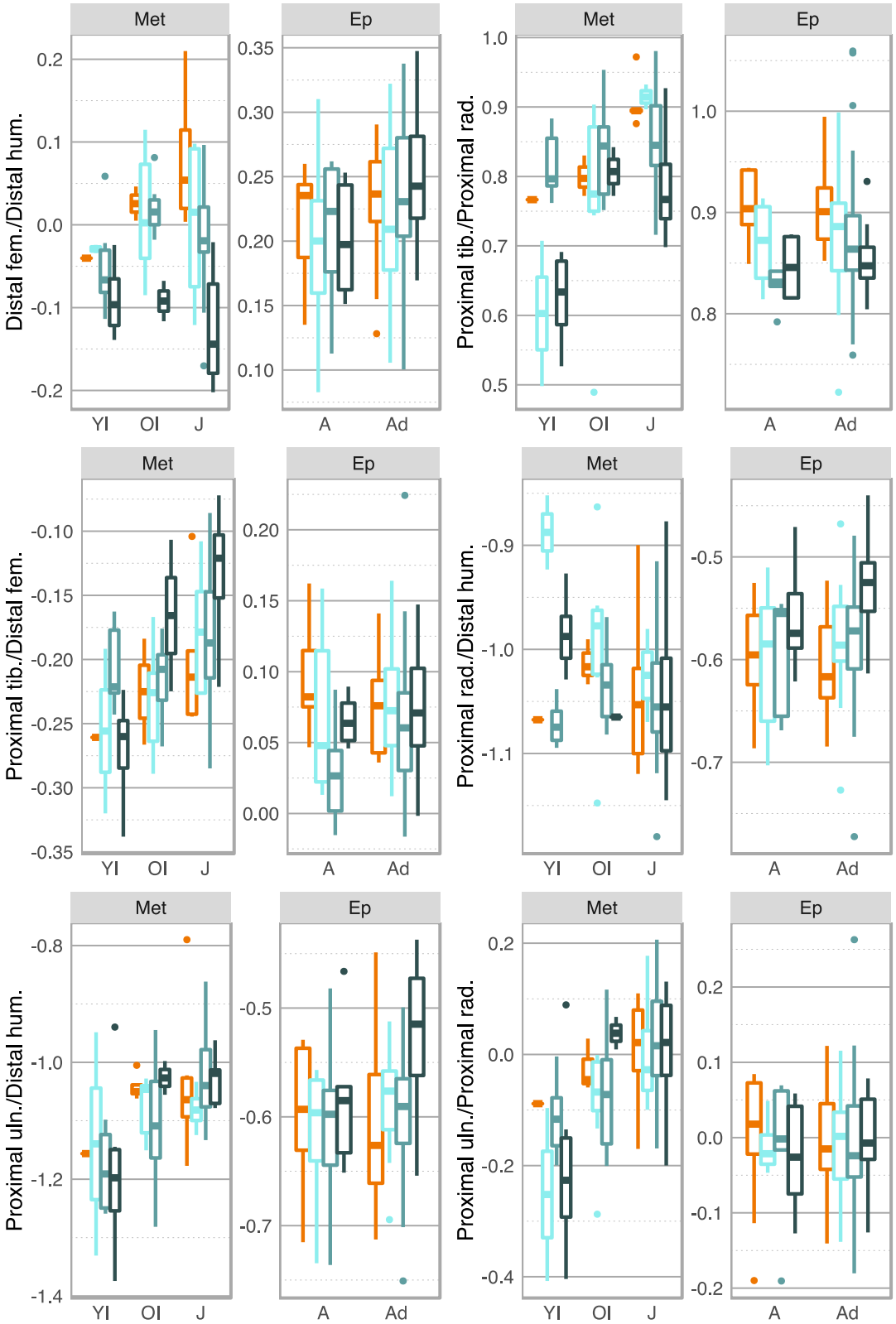

Figure 3.27 Joint (Ep) and metaphyseal (Met) ratios within each age group for P. paniscus*, and* P. troglodytes *subspecies. Color key same as Figure 3.26; See Table 3.18 for significant differences.*

3.3.2.3 Summary

In general, there are relatively few ontogenetic differences found in joint and metaphyseal measurements. Patterns of taxonomic differences are essentially similar in both epiphyses and metaphyses. In absolute measurements, more differences are found in the forelimb than in the hind limb: the distal humerus and/or proximal radius measurements are significantly smaller in bonobos than common chimpanzees as a whole in all three of the age groups tested, but no hind limb joints or metaphyses reach statistical significance. This is also true for comparisons between subspecies, although no individual subspecies differs significantly from bonobos in the adolescent age group, and only *P. t. troglodytes* and *P. t. verus* were found to differ from bonobos in old infants and juveniles. No *P. troglodytes* subspecies differed significantly from each other in raw joint measurements.

Ratios show even fewer significant differences than absolute measurements, and differences were found only in inter-limb ratios. The distal tibia/proximal radius showed significant differences across species and between *P. paniscus* and *P. t. troglodytes* in adolescence, with relatively higher values (i.e., relatively larger tibial plateau/smaller radial head) in the former. The distal femur/distal humerus also was transiently different between *P. t. troglodytes* and *P. t. verus* in juveniles – the only intra-species difference found.

3.3.3 Comparison to behavioral data and Discussion

It was originally hypothesized that joint ratios would, like limb lengths, broadly follow phylogenetic patterns rather than behavior. Previous studies of joint ratios at larger taxonomic scales suggest that relatively large femoral and/or humeral heads may relate to

the use of the fore- or hind limbs in more variable positions necessary for the types of arboreal behaviors practiced by large-bodied hominoids (Ruff, 1988; 2002; Hammond, 2014). These studies have found that larger forelimb joint surfaces compared to hind limb joint surfaces distinguish hominoids from cercopithecoids and, within hominoids, often separate *Pongo* and *Hylobates* from the more terrestrial knuckle-walking *Gorilla* and *Pan* (Ruff, 2002).

The present study finds that in adult *Pan*, hind limb joints tend to be relatively and absolutely larger in bonobos than in common chimpanzees, but that these differences are less pronounced or even absent earlier in development. (Interestingly, while the proximal femur and humerus and proximal tibia and radius show more pronounced differences, there is substantial overlap in the distal femur and humerus ratios). If these ratios relate to the varied limb positions necessary for arboreal substrate use, these patterns are difficult to reconcile with new behavioral data suggesting that *P. paniscus* are not substantially different from other *Pan* in overall arboreal behavior (Table 2.7). They could be explained by subspecies differences in types of behaviors *within* arboreal locomotion, i.e., if bonobos practice more arboreal quadrupedalism and less forelimb-dominated climbing and suspension even when on arboreal substrates, then having relatively smaller forelimb joint surfaces might be expected. However, the reverse is actually true: frequencies of climbing and suspension on arboreal substrates are similar to or higher than those found in other *Pan* (Table 2.7, Table 2.8). Similarly, the direction of ontogenetic change in these ratios (where they appear to change at all) is the opposite of what would be predicted based on declining rates of suspensory arboreal behavior with

age. These observations are consistent with the hypothesis that joints are not developmentally plastic.

Comparisons involving the distal humerus also consistently showed differences among the four taxa in adults, although these were not found during ontogeny. Compared to all other taxa, *P. paniscus* were also found to have a relatively large distal humerus compared to proximal humerus, and *P. t. verus* were found to have relatively small distal humeri compared to both their proximal radius and ulna. These results are unexpected. As there are no differences in radial to ulnar ratios between taxa, it is difficult to imagine how there could be such systematic differences in opposing sides of the same joint. It is possible that these results are due to measurement technique. Differences in the non-articular portion of the distal humerus may be impacting data, as the measurement of the proximal ulna is not an exact representation of the true M-L breadth of the surface or of the corresponding articular surface on the trochlea of the humerus.

There were also several instances in which *P. t. troglodytes* differed from another *P. troglodytes* subspecies. These differences are difficult to explain in the absence of further genetic and behavioral data. However, despite this, the preponderance of differences in joint and metaphyseal morphology systematically differentiates *P. paniscus* from other *P. troglodytes* and do not generally match variation in behavioral data. This is consistent with the hypothesis that joint morphology is relatively phylogenetically conservative and not developmentally plastic.

3.4 SUMMARY

Based on the hypothesis that bone lengths and joint dimensions are primarily genetically determined, but cross-sectional properties are more developmentally plastic, it was predicted that lengths and joint sizes, and ratios derived from them would primarily vary along phylogenetic lines, and that ratios would be fairly constant over life, while cross-sectional parameters would more closely track behavioral differences between taxa regardless of phylogenetic affiliation. This study found that both lengths and length ratios and joint sizes and joint size ratios did not vary in a manner consistent with hypothesized functional relationships with behavior. Instead, these variables tracked phylogenetic differences between taxa or followed other patterns that are not consistent with current understandings of either genetic relationships or behavioral variation. Cross-sectional strength ratios and shape ratios, on the other hand, more closely tracked behavioral data both across and within taxa on the whole, but did not always follow predicted patterns. Interpretation of both morphology and behavior is complicated by a paucity of available specimens for bonobos in key age groups (early infancy and adolescence), as well as by incompletely understood behavioral variation among chimpanzees, including geographic variation within subspecies, as mentioned earlier and discussed further in Chapter 5.

4 RESULTS: HAND AND FOOT BONE CURVATURE AND METACARPAL AND METATARSAL HEAD SHAPE

This chapter covers measurements of the shapes of hand and foot bones, including 1) Hand and Foot Bone Curvature, and 2) Metacarpal and Metatarsal Head Shape. As in the previous chapter, each section begins with a table summarizing the variables discussed, followed by analyses of variation across adults and during ontogeny. Each section concludes with a discussion of how well this morphological variation tracks behavioral differences.

4.1 CURVATURE

This section covers curvature of the hand and foot bones. As discussed in the Materials and Methods, curvature was assessed in two ways: first, using Included Angle (IA, based on modeling the bone as an arc along a circle's circumference), and second, using Normalized Curvature Moment Arm (NCMA, the ratio of the curvature moment arm to the AP cross-sectional bending strength of the bone) (see Section 2.2.3). Variables and abbreviations discussed in this section are found in Table 4.1. All variables were natural log-transformed for adults for statistical reasons but were analyzed in unlogged space for ontogenetic comparisons because statistics for these do not assume normality (logging NCMA measurements results in simpler polynomial models but does not alter results).

Table 4.1 Curvature variables

Variable*	Abbreviation
Included Angle (IA)	
3rd Metacarpal IA	MCIA
3rd Metatarsal IA	MTIA
3rd Proximal phalangeal IA	PIA
Normalized Curvature Moment Arm (NCMA)	
3rd Metacarpal NCMA	MCNCMA
3rd Metatarsal NCMA	MTNCMA
3rd Proximal phalangeal NCMA	PNCMA

**Calculated as described in Materials and Methods Section 2.2.3*

4.1.1 Adults

4.1.1.1 Species-level analyses

Table 4.2 contains summary statistics for IA and NCMA values in *P. paniscus* and *P. troglodytes*. Two sample t-tests with unequal variance or Mann-Whitney U tests (in the case of MTIA, which was not normally distributed) were used to test for sex differences within species, with Bonferroni-corrected significance levels ($\alpha < .05/2$). Note that sample sizes of the two measurement methods occasionally differ due to difficulty in measuring internal geometry or missing elements (in the case of PNCMA, which requires both a phalanx and a metacarpal; see methods).

Table 4.2 Summary statistics for and sex differences in curvature in adults (species)

	P. paniscus						***P. troglodytes***					
	Male			**Female**			**Male**			**Female**		
Variable	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**
MCIA	7	38.98	5.72	10	39.02	4.14	28	37.79	4.90	36	38.35	4.96
MTIA	7	43.41	5.02	10	44.42	2.66	27	44.44	4.99	36	45.86	4.81
PIA	5	58.68	5.09	9	57.63	6.58	21	56.72	6.43	28	53.03	8.97
MCNCMA	7	0.77	0.14	10	0.80	0.21	28	**0.55**	0.12	36	**0.68**	0.17
MTNCMA	7	1.20	0.24	10	1.30	0.29	26	**0.84**	0.23	36	**1.03**	0.21
PNCMA	5	1.12	0.17	9	1.15	0.32	21	0.82	0.18	25	0.91	0.22

Bold values are significantly different between males and females within species

No Included Angle measurements were different between sexes, but both metacarpal and metatarsal NCMA were significantly larger in female *P. troglodytes* than in males. Accordingly, for all analyses, these two variables were analyzed separately in males and females.

Figure 4.1 shows box and whisker plots for curvature measurements. Species differences were tested with two sample t-tests with unequal variance if variables were normally distributed (or Mann-Whitney U tests in the case of MTIA; see above). For MC and MTNCMA, which were analyzed separately in males and females, significance levels were Bonferroni adjusted ($\alpha < .05/2$). IA measurements are not significantly different between species, although metacarpal and phalangeal curvature are both slightly higher in *P. paniscus*, and there is substantial variation within *P. troglodytes* in these measurements, especially in the phalanx.

NCMA, in contrast, is significantly higher in *P. paniscus* than in *P. troglodytes* in all comparisons. This seems to be primarily driven by differences in cross-sectional properties rather than curvature moment arm: metacarpal and metatarsal Zx are both significantly different between species even after sex differences are taken into account (two-way ANOVA, $p < .05$), but the three curvature moment arms are not.

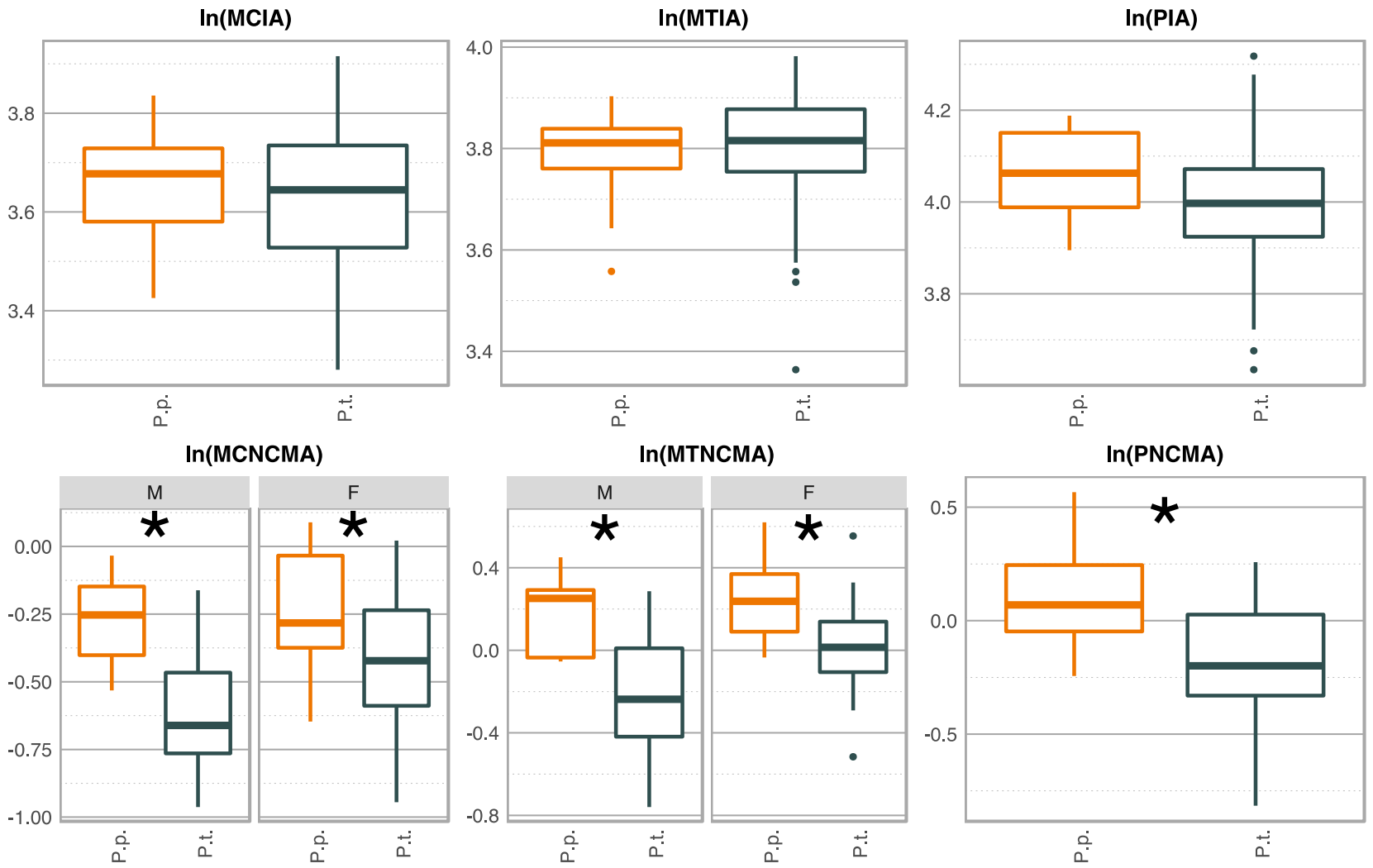

Figure 4.1 Boxplots of curvature in P. paniscus (P.p.) *and* P. troglodytes (P.t.). *Significant differences are indicated with asterisks.*

4.1.1.2 Subspecies-level analyses

Prior to analyses of subspecies differences, sex differences within each subspecies were tested, except for in *P. t. schweinfurthii*, for which sample sizes were too small (sample sizes, means, and standard deviations of each variable are found in Table 4.3). Sex differences were analyzed with t-tests with unequal variance, except for metatarsal IA, which was analyzed with Mann-Whitney U tests (see above). Alpha values were Bonferroni adjusted to adhere to a family-wise error rate of .05 for each variable. Metatarsal NCMA and phalangeal IA were significantly different between sexes in at least one of the subspecies (Table 4.3), so subspecies differences for these variables were analyzed separately in males and females.

Box and whisker plots of curvature measurements are shown in Figure 4.2. One-way ANOVAs were used to test for species differences (or Kruskal-Wallis tests, for metacarpal curvature, which was not normally distributed). Games-Howell tests were then used to test for pairwise differences between species, at a family-wise error rate of .05.

As with species-level analyses, differences in IA curvature measurements are less pronounced than differences in NCMA. It is clear that *P. troglodtyes* subspecies vary in NCMA values, with *P. t. schweinfurthii* generally closer to *P. paniscus* than the other two subspecies. These differences are statistically significant in the metacarpal and phalanx (Figure 4.2). Interestingly, in metatarsal NCMA, males seem to show a slightly different pattern, with *P. t. troglodytes* having lower values than other taxa, reaching significance in comparisons with *P. t. verus*.

Table 4.3 Summary statistics for and sex differences in curvature in adults (subspecies)

	P. t. schwein.						***P. t. trog.***						***P. t. verus***					
	Male			**Female**			**Male**			**Female**			**Male**			**Female**		
Variable	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**
MCIA	2	39.37	5.34	6	40.92	2.29	18	37.20	4.72	19	36.15	5.12	8	38.71	5.66	11	40.75	4.08
MTIA*	2	48.22	7.65	6	46.30	4.53	18	42.72	4.68	19	45.05	5.31	7	47.76	3.08	11	47.02	4.15
PIA	0	NA	NA	2	51.58	9.58	17	56.16	6.89	17	53.62	10.73	4	**59.08**	3.60	9	**52.25**	5.27
MCNCMA	2	0.55	0.05	6	0.86	0.17	18	0.54	0.13	19	0.64	0.16	8	0.57	0.10	11	0.66	0.13
MTNCMA	2	0.92	0.38	6	1.13	0.09	17	**0.76**	0.21	19	**1.01**	0.26	7	1.02	0.13	11	0.99	0.12
PNCMA	0	NA	NA	2	1.10	0.07	17	0.81	0.19	17	0.92	0.24	4	0.84	0.14	6	0.81	0.16

**Not normally distributed, see text for details of analysis*
Bold values are significantly different between males and females within subspecies

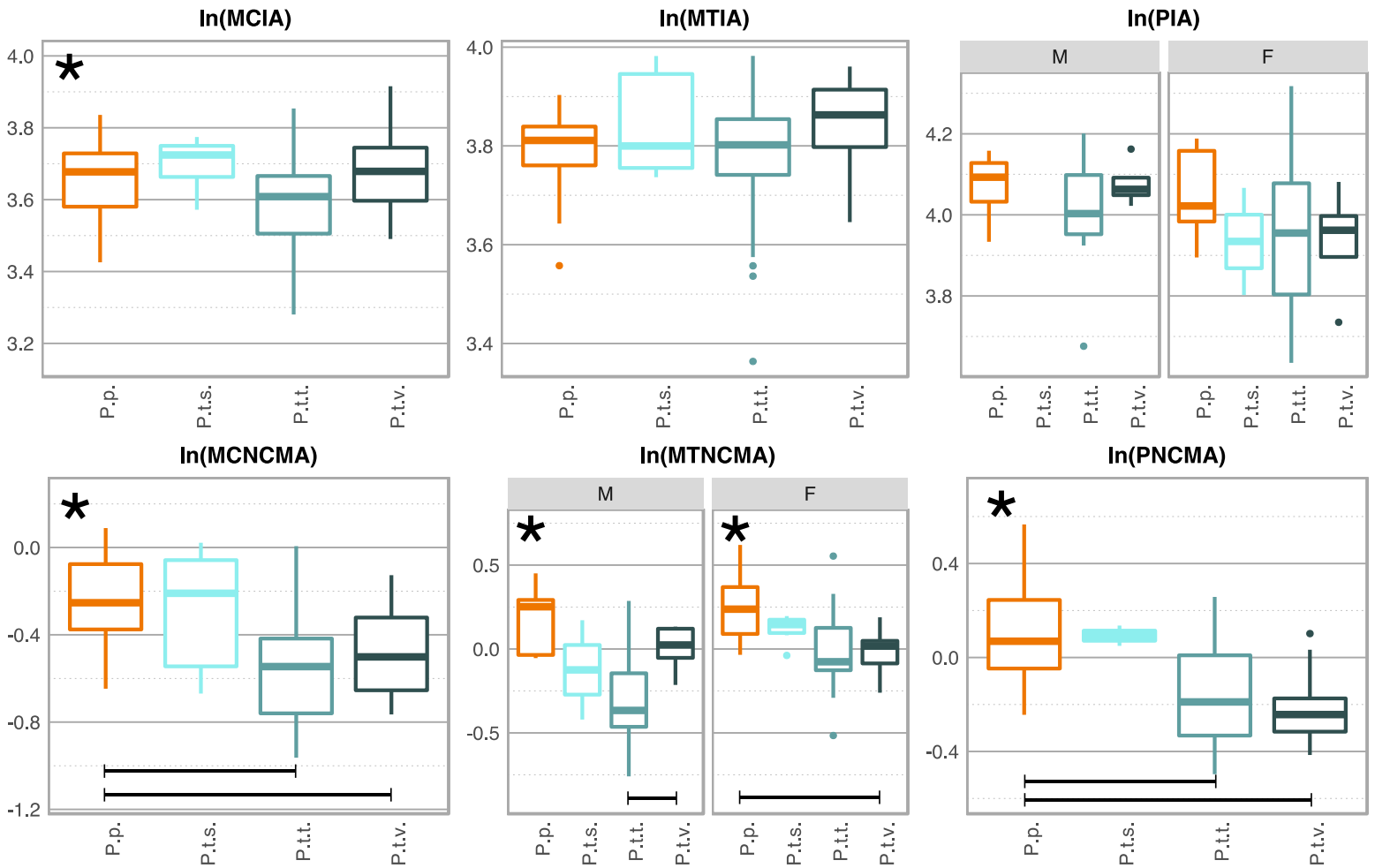

Figure 4.2 Curvature in adult P. paniscus *(P.p.),* P. t. schweinfurthii *(P.t.s.),* P. t. troglodytes *(P.t.t.), and* P. t. verus *(P.t.v.). Significant overall differences between taxa (within sexes) are indicated with large black asterisks; significant post-hoc comparisons are indicated with brackets.*

4.1.1.3 Summary

In summary, there are relatively few sex differences in any curvature measurements in *Pan* and no evident systematic patterning to these differences where they occur. Overall, differences in NCMA are much more pronounced than differences in curvature measured with Included Angle, which does not tend to significantly differ between taxa. Where differences exist in either IA or NCMA, *P. paniscus* generally has higher values than *P. troglodytes* as a whole but *P. t. schweinfurthii* are actually closer in mean value to *P. paniscus* than they are to other *P. troglodytes*. It should be noted that a similar pattern of higher values in bonobos is seen in phalangeal curvature as measured by IA. However, *P. t. troglodytes* females show an extremely large range of variation, encompassing both the lowest and the highest phalangeal curvature values for *P. troglodytes* as a whole within their ranks (see Comparison to Behavioral Data). In general, though, it seems clear that bonobos tend to have more curved hand and foot bones relative to the bending strength of those bones than both *P. t. troglodytes* and *P. t. verus*, but not necessarily *P. t. schweinfurthii.*

4.1.2 Ontogenetic

4.1.2.1 Overall correlations with age

Spearman correlations for curvature values against estimated age are found in Table 4.4. One *P. t. verus* (MPI 11787) had substantially higher values for metacarpal and phalangeal NCMA than all other individuals (13.18 and 26.45 respectively, when the next highest were 5.66 and 14.98). This is driven by an unusually low Zx value in the

metacarpal, as IA and curvature height measurements were well within normal ranges. Because this individual is an extreme outlier and is highly statistically influential (as determined by Cook's Distance, which is over ten times larger in this specimen than the mean Cook's Distance score for all individuals), it was excluded from these analyses. The same individual was not an outlier for other analyses involving ratios of metacarpal cross-sectional geometry, so was not excluded from these.

Directionality and significance of trends against age are generally consistent across taxa, with some exceptions. Curvature as assessed by IA increases significantly with age in both the metatarsal and metacarpal in all but *P. t. troglodytes*, while phalangeal curvature does not significantly change with age in any taxon *except P. troglodytes* and *P. t. troglodytes* in particular, where it declines. (IA also declines in *P.t. verus*, but this does not reach significance.) NCMA, on the other hand, significantly *decreases* with age in all taxa and skeletal elements. Because it is likely that these patterns are complex and therefore not well described with simple correlations, additional analyses were performed to take potential non-linear change into account.

Table 4.4 Correlations and significance for curvature with age

	P. paniscus	***P. troglodytes***	***P. t. schwein.***	***P. t. trog.***	***P. t. verus***
Variable	**rho***	**rho**	**rho**	**rho**	**rho**
MCIA	**0.67**	**0.62**	**0.71**	**0.50**	**0.78**
MTIA	**0.61**	**0.50**	**0.76**	0.23	**0.72**
PIA	-0.15	**-0.30**	0.32	**-0.38**	-0.44
MCNCMA	**-0.86**	**-0.90**	**-0.86**	**-0.91**	**-0.92**
MTNCMA	**-0.86**	**-0.92**	**-0.87**	**-0.94**	**-0.95**
PNCMA	**-0.84**	**-0.94**	**-0.91**	**-0.94**	**-0.91**

** bolded values are significant at $p < .05$*

4.1.2.2 Species-level analyses

Changes with age were evaluated at a finer level by fitting polynomial models to the sample, as described in the Methods. Species differences were tested by fitting a polynomial to the pooled common chimpanzee sample, then calculating bonobo residuals from this fitted line and using Wilcox rank-sum tests to test whether these significantly differed from zero. This section covers non-adults only (see previous section for adults).

Table 4.5 Means and (SD)'s of curvature in each species/age cohort

	Young Inf. (0-2y)				**Old Inf. (2-5y)**			
	P. pan.		***P. trog.***		***P. pan.***		***P. trog.***	
Variable	*n*	*mean(SD)*	*n*	*mean(SD)*	*n*	*mean(SD)*	*n*	*mean(SD)*
MCIA	1	32.33 (NA)	13	27.92 (3.22)	3	27.74 (5.32)	14	28.22 (3.89)
MTIA	1	34.48 (NA)	12	35.56 (4.72)	2	35.01 (4.76)	13	35.85 (5.76)
PIA	1	55.71 (NA)	13	61.73 (6.16)	2	61.83 (2.75)	12	60.05 (7.16)
MCNCMA	1	4.65 (NA)	11	4.61 (0.78)	3	3.65 (0.15)	14	2.93 (0.77)
MTNCMA	1	10.66 (NA)	12	9.94 (2.47)	2	6.13 (0.09)	13	5.56 (2.00)
PNCMA	1	8.01 (NA)	11	10.74 (2.22)	2	7.84 (0.91)	12	6.45 (2.41)
	Juv. (5-10y)				**Adol. (10-14y)**			
MCIA	6	31.71 (4.48)	39	32.23 (4.06)	8	37.23 (3.22)	18	35.68 (4.05)
MTIA	6	39.67 (6.29)	33	40.32 (5.03)	8	42.78 (3.54)	17	43.88 (8.58)
PIA	4	61.17 (5.41)	31	56.04 (7.74)	7	59.22 (5.22)	12	59.34 (6.43)
MCNCMA	6	1.74 (0.42)	39	1.49 (0.51)	8	0.93 (0.20)	18	0.70 (0.21)
MTNCMA	6	2.69 (0.78)	33	2.34 (0.77)	8	1.33 (0.28)	17	1.14 (0.49)
PNCMA	4	3.29 (1.13)	31	2.63 (0.95)	7	1.48 (0.43)	12	1.12 (0.25)

None are significantly different between species at family-wise alpha of .05

Curvature as measured by IA against age is always best fit by a simple first order (linear) polynomial model, while NCMA is best fit by either second (MC, P) or third (MT) order polynomials. Despite the minor difference in polynomial fit between elements, NCMA changes similarly in all bones: values are highest in infants and decline steadily up until about age 10, when essentially adult values are reached (see Figure 4.3a for example). Since NCMA involves scaling by bending strength, these patterns are likely to be at least partially a function of ontogenetic change in the values used for that normalization. There is more scatter in IA values, which decrease only slightly with age in the phalanx but increase in both the metacarpal and metatarsal (see Figure 4.3b).

Means and standard deviations of variables, and significant differences between species within each age group as calculated from model residuals, are found in Table 4.5. Curvature values measured by IA are fairly similar between taxa at similar ages, and differences never reach statistical significance. NCMA values tend to be somewhat higher in *P. paniscus* than in *P. troglodytes*, but again, these differences are never significant.

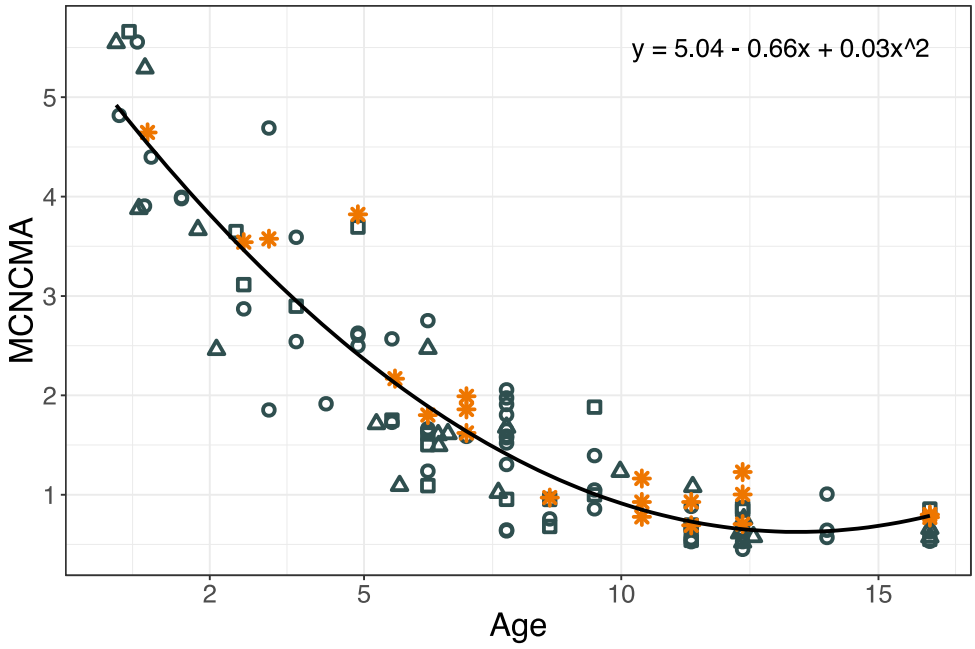

Figure 4.3a Growth in metacarpal NCMA in P. paniscus *(orange) and* P. troglodytes *(blue) Line fit through pooled sample.*

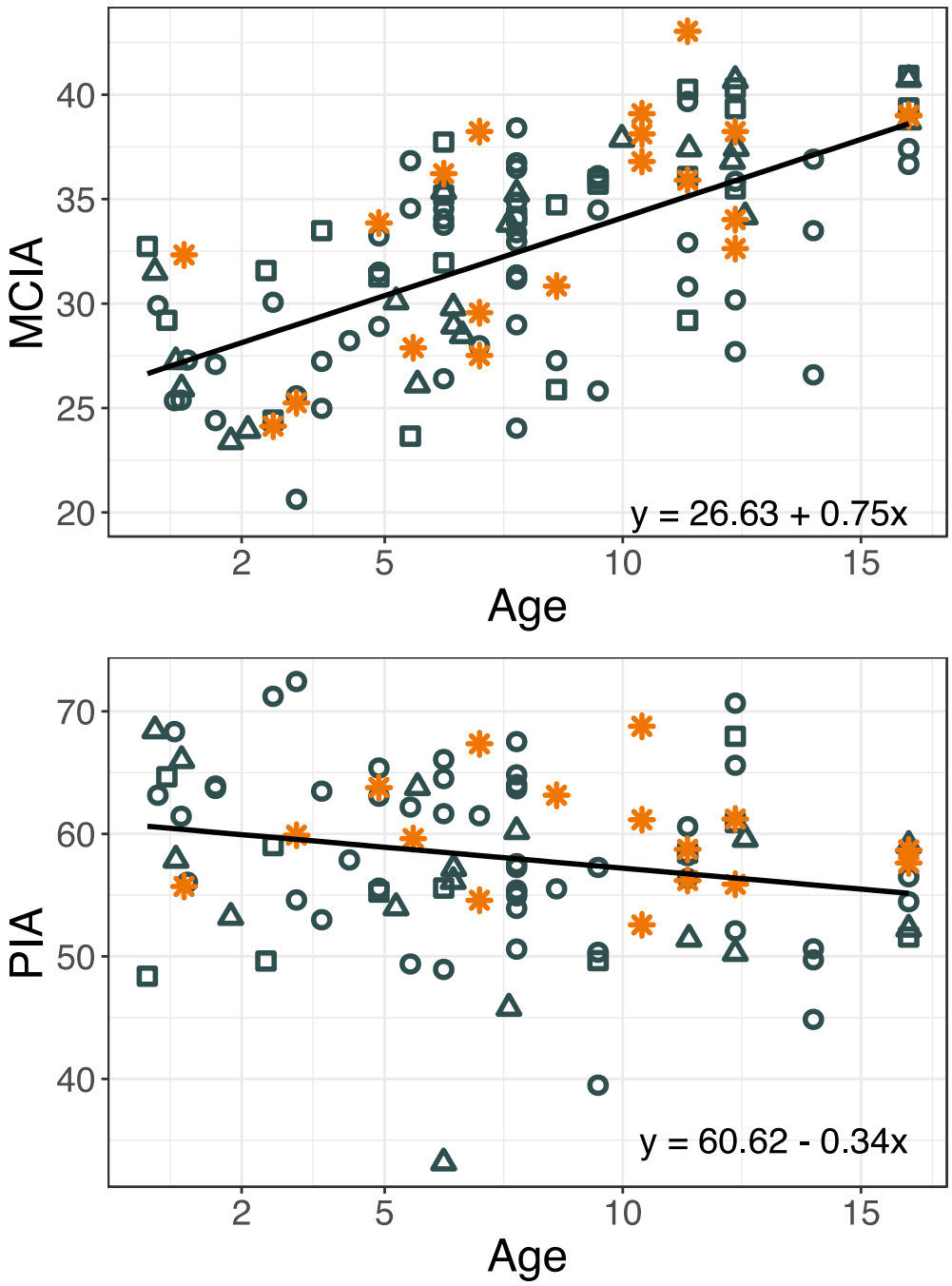

Figure 4.3*b Growth in metacarpal and phalangeal Included Angle (IA) in* P. paniscus *(orange) and* P. troglodytes *(blue) Line fit through pooled sample. Metatarsal not shown.*

4.1.2.3 Subspecies-level analyses

For this section, the same variables analyzed between species were visualized with LOWESS fits and statistically analyzed by testing for differences in residuals for

each subspecies and for bonobos from a line fit to the total pooled data scatter using Bonferroni adjusted pairwise Wilcox rank-sum tests. Plots of NCMA and IA against age are found in Figure 4.4, with complete summary statistics for each variable summarized in the Appendix. Again (see previous section), first order polynomials are the best fits for IA measurements, and either second or third order polynomials are the best fits for NCMA.

As in species-level comparisons, ontogenetic trajectories for NCMA appear fairly similar in all taxa, with highest values in infancy declining to adult-like values by around age 10. Metacarpal and metatarsal IA show a general increase with age, and phalangeal curvature a slight decrease, but overall there is substantial scatter around these trends amongst all four of the taxa considered, making it difficult to discern systematic taxonomic differences. There are no significant differences between any of the four taxa in any age group in either NCMA or in IA measurements.

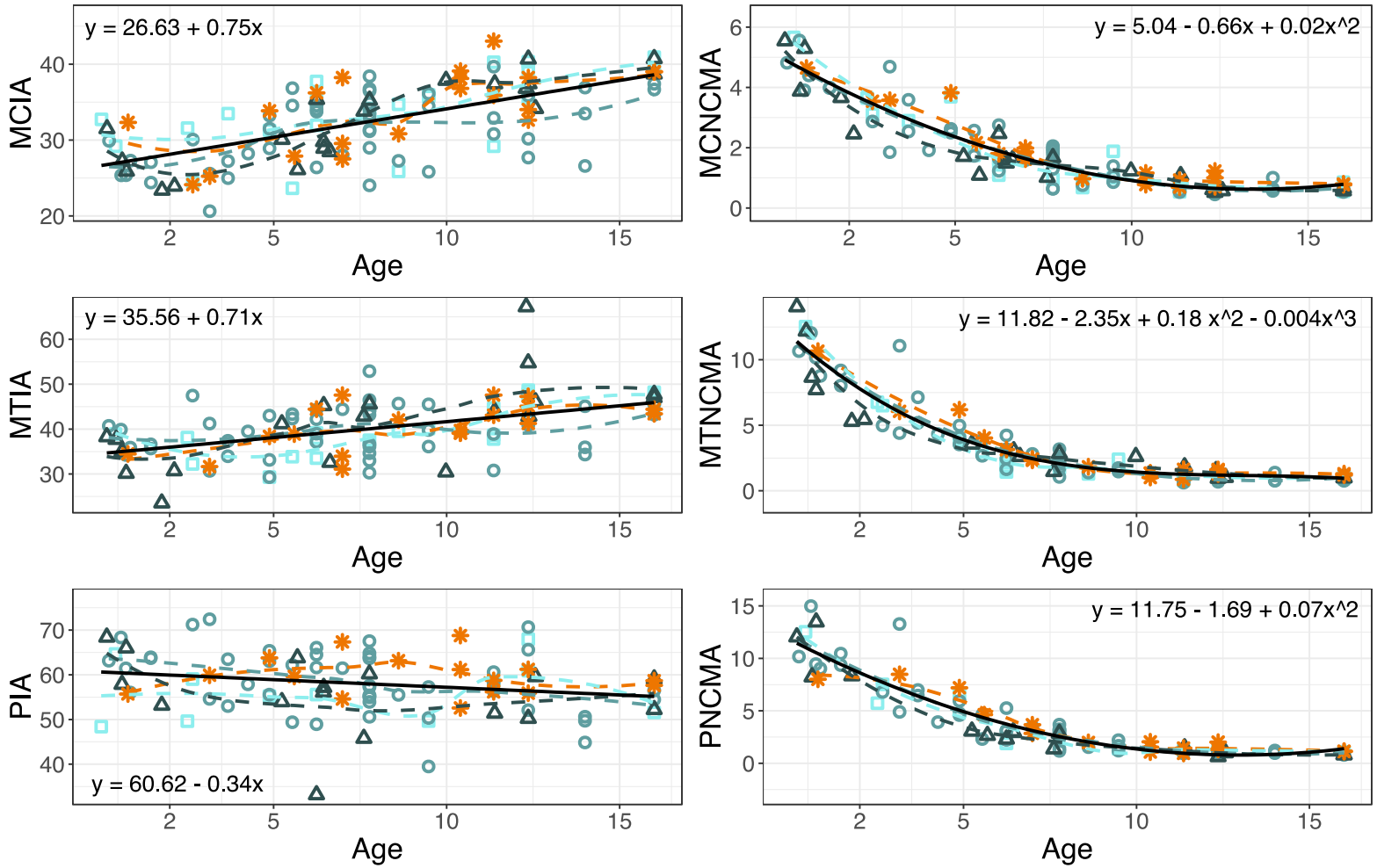

Figure 4.4 Growth in curvature in P. paniscus *(orange stars) and* P. troglodytes *subspecies (blue;* P. t. schweinfurthii = *squares,* P. t. troglodytes = *circles,* P. t. verus = *triangles). Black line = pooled total sample equation, dashed lines = LOWESS fits for visualization of taxon-specific trends.*

4.1.2.4 Summary

In summary, curvature as measured by Included Angle (IA) tends to increase with age in the metacarpal and metatarsal in *Pan* overall. Phalangeal IA does not show a similarly consistent trend and while change with age is significant in *Pan* overall and in some individual taxa, the amount of change is very slight. NCMA shows different ontogenetic patterns and is highest in infancy and decreases with age in all three bones, which is likely driven primarily by age-related increases in cross-sectional geometry (see next section). Although there is some variation around these general trends, contrary to predictions, there are no significant differences between taxa within any of the age categories, either at the species or the subspecies level.

4.1.3 Comparison to behavioral data and discussion

There are two separate hypotheses about how manual and pedal bone curvature relates to behavior: the first, that phalangeal curvature is related to frequencies of arboreality and/or manual suspension, and the second, that metacarpal (but not metatarsal) curvature is related to frequencies of knuckle-walking (Hypotheses 2 and 3).

As discussed in the Introduction, in adults, *P. paniscus* seem to exhibit less quadrupedal behavior and more irregular climbing and scrambling behavior in arboreal contexts compared to *P. troglodytes*, but overall frequencies of arboreal behavior in general are higher among *P. t. verus*. Knuckle-walking behavior specifically has not been as consistently documented as the broader behavioral categories included in the behavioral overview, but differs both between adults and during ontogeny, where it has been studied: when walking quadrupedally (at least during arboreal locomotion), bonobos

have higher frequencies of palmigrade quadrupedalism than *P. t. verus*, with *P. t. schweinfurthii* (the Mahale and Gombe populations) more similar to the former than the latter (Table 4.6). It is important to bear in mind that within each taxon males generally practice less arboreal quadrupedalism overall, and that differences in the amount of the total behavioral repertoire taking place arboreally will impact the overall frequencies of specifically arboreal behaviors.

Table 4.6 Frequencies of hand postures in arboreal quadrupedalism in adults

		Frequency*	
Taxon	**Sex**	**KW**	**PG**
P. t. schweinfurthii	M	23.3	76.7
	F	6.3	93.8
P. t. verus	M	72.7	27.3
	F	57.1	42.9
P. paniscus	M	17.0	83.0
	F	13.0	87.0

** Frequency of knuckle walking (KW) and palmigrade (PG) quadrupedalism in arboreal contexts. Data from Doran & Hunt 1994, Table 7.*

The frequency of knuckle walking behavior also increases with age in at the Ngogo population of *P. t. schweinfurthii* relative to use of other hand postures such as grasping (which occurs during quadrupedal locomotion on an arboreal substrate) or palmigrade quadrupedalism (Table 4.7). This seems to be related both to increased frequencies of terrestrial quadrupedalism with age and to ontogenetic shifts in the types of quadrupedalism preferred. In this population, all terrestrial quadrupedal locomotion was knuckle walking, regardless of age. However, during arboreal quadrupedalism, frequencies of knuckle walking are lowest in infants and increase from infants to juveniles and again from juveniles to adolescents. Arboreal palmigrade walking

concurrently decreases, and was not observed at all in adolescents or adults. Although there are no corresponding ontogenetic data for other taxa, it is likely that they also increasingly prefer knuckle-walking quadrupedalism as they mature: most primates gradually acquire adult-like locomotor profiles with age (including in specific kinematic aspects of knuckle walking (Inouye, 1994a)), and increased overall terrestriality affords more opportunities for this type of locomotion. It should be noted that because the amount of terrestrial quadrupedalism relative to other types of locomotor behavior also increases with age (and, as discussed above, terrestrial quadrupedalism in this population was exclusively knuckle walking), the increase in arboreal knuckle walking depicted in Table 4.7 likely substantially under-represents the actual increase in overall frequencies of knuckle walking behavior relative to both other types of quadrupedal hand postures and to locomotor behavior in general.

Table 4.7 Frequencies of hand postures in arboreal quadrupedalism during ontogeny in Ngogo P. t. schweinfurthii

		Frequency*	
Age	**KW**	**GR**	**PG**
Young inf (0.1-3.0y)	12.9	68.6	18.5
Old inf (3.1-5.0y)	30.8	47.8	21.4
Juv (5.1-10y)	41.5	56.5	2
Adol (10.1-13y)	50.3	49.7	0
Adult (20.0+y)	73.7	26.3	0

**Frequency of knuckle walking (KW), grasping (GR), and palmigrade (PG) hand postures as percentage of total hand postures during arboreal quadrupedalism (terrestrial quadrupedalism is 100% knuckle walking in all age categories). Derived from* (Sarringhaus, 2013a)*, Fig. 3.6*

Thus, both types of curvature were predicted to change with age. Phalangeal curvature was predicted to decrease. Metacarpal (but not necessarily metatarsal) curvature as measured by Included Angle was predicted to increase, based on past studies

showing higher levels of curvature in knuckle-walking taxa (Sarringhaus, 2013a). Curvature as measured by NCMA should be interpreted slightly differently: higher NCMA values indicate that the bone is relatively weaker against bending created by compressive axial forces, so if the primary function of curvature is to decrease strain, increasing levels of knuckle walking should be associated with a *decrease* in curvature measured by NCMA. A lack of change or an increase in NCMA with age may indicate that strain may not be the major determining factor of this morphology.

There should also be differences among adults, with *P. t. verus* having the most curved phalanges as measured with IA (in keeping with their higher frequencies of arboreal and suspensory behavior). It is less easy to generate predictions for metacarpal and metatarsal curvature differences among adults given the lack of overall (rather than solely arboreal) data on knuckle walking frequencies, but given that *P. t. verus* show substantially more arboreal knuckle walking than the other two taxa as well as overall more arboreal behavior, it seems reasonable that they might also have more curved (Included Angle) metacarpals that are relatively stronger against axial compressive forces (lower NCMA), as is found in the current study.

4.1.3.1 Phalangeal curvature

Adult bonobos were found to have slightly higher phalangeal curvature as measured by Included Angle (as found previously, (Susman, 1979; Stern and Susman, 1983; Susman et al., 1984; Stern et al., 1995)). However, this difference is not statistically significant. This is in part because there is a large amount of variation in *P. troglodytes* and specifically in *P. t. troglodytes* in phalangeal curvature, with both the largest and smallest curvature values found within this taxon (Figure 4.5)

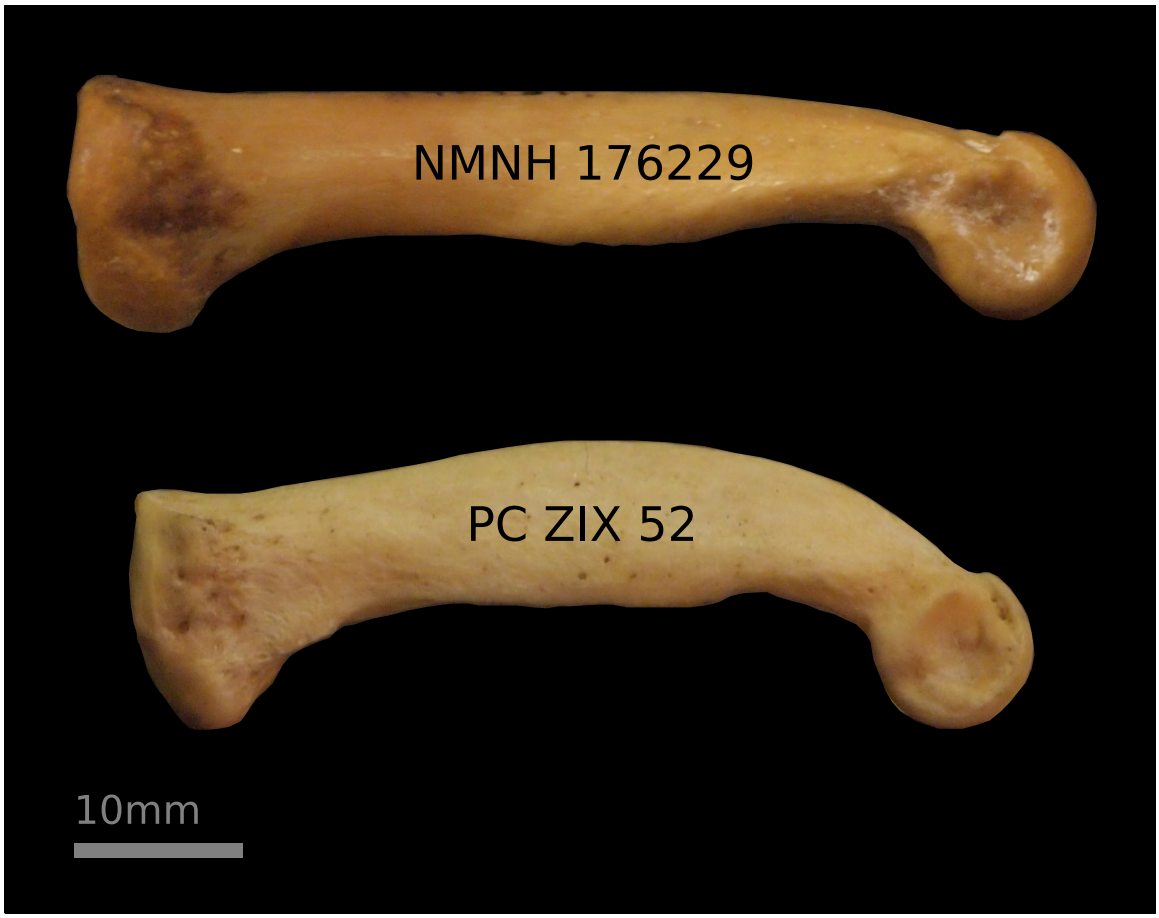

Figure 4.5 Example of extremes of phalangeal curvature in P. troglodytes*. Both are female* P. t. troglodytes*; IA's are 75.01 and 37.90 and NCMA's are 1.29 and 0.44, respectively.*

The source of this variation is unclear. It does not appear to be related directly to body size – correlations of phalangeal IA with body size (not shown) were not significant either in *P. troglodytes* as a whole or in *P. t. troglodytes* specifically, or in females separately within each of these two taxonomic groups. We lack behavioral data for *P. t. troglodytes*, so cannot rule out extreme behavioral variation within this taxon, but variation does not appear to be geographically patterned according to museum records for specimen localities. This is also a very different signal than that found in cross-sectional

properties, which are also purported to reflect behavior but do not show the same degree of morphological variation within *P. t. troglodytes*.

This high variation among adults is accompanied by relatively less change in phalangeal curvature measured during ontogeny, despite sizable age-related decreases in the frequencies of behaviors purported to increase phalangeal curvature. There is evidence for a slight, but statistically significant, decline in phalangeal curvature overall within *P. troglodytes*, although declines within individual subspecies and within *P. paniscus* are not significant, with the exception of *P. t. troglodytes*. It is possible that there are more subtle changes in curvature that are not captured by the relatively gross technique of modeling the arc of the phalanx as a circle (Deane and Begun, 2010), or that phalangeal curvature does not have as strong a relationship to behavior as has been previously suggested, at least when using this measurement technique (see Discussion). Results from NCMA analyses clarify this somewhat: *P. t. verus* tend to have lower values than both bonobos and *P. t. schweinfurthii (*significantly so in the former), suggesting that their bones are better reinforced against AP bending compared to the load arm. This is in accordance with predictions based on arboreal behavior in adults, and the substantial decreases in phalangeal NCMA during ontogeny are also consistent with decreases in arboreal behavior, but results for NCMA in the metacarpal and metatarsal are not consistent with predictions based on knuckle walking frequencies (see next section).

4.1.3.2 Metacarpal and metatarsal curvature

Metacarpal and metatarsal curvature as measured by Included Angle also shows fewer differences between taxa than would be predicted based on hypothesized relationships with knuckle walking. Across adults, there are no differences in IA at either

the species or the subspecies level, despite purported differences in frequencies of knuckle-walking behavior (at least in arboreal settings, Table 4.6). It is possible, however, that arboreal knuckle walking is actually not a primary driver of this morphology. The actual underlying frequencies of knuckle walking behavior relative to the total behavioral repertoire are likely more similar across taxa than those in solely arboreal contexts, as both qualitative and quantitative studies have suggested that knuckle walking makes up the vast majority of terrestrial quadrupedalism in adults and these subspecies show some variation in overall amounts of arboreal behavior.

While curvature of both bones increases with age in all taxa (even after taking the increased contribution of the epiphyses into account via the transformation equations discussed in the Methods section), there are no noticeable differences in the rate or degree of this increase between species or subspecies. Comparing metacarpal curvature to ontogenetic change in knuckle walking behavior in the one taxon in which it is documented (*P. t. schweinfurthii*) finds that both metacarpal IA and the frequency of knuckle walking behavior (relative to other types of arboreal quadrupedalism) increase with age (Figure 4.6), confirming the results of the Sarringhaus's (2013) study. Metatarsals, which are not loaded in the same manner as the metacarpals, also increase in IA curvature with age (see section 4.1.2.3).

Thus, while metacarpal IA changes during ontogeny in a manner consistent with predictions, IA curvature variation across adults does not seem to track behavior as well. It is possible that overall frequencies of knuckle waking behavior, rather than solely arboreal, would result in better matching. However, the similarity in variation (or lack of variation) in metacarpal and metatarsal curvature during ontogeny and across adults,

despite the very different loading regimes expected between the two, suggests that this feature may instead be developing in response to other factors, either genetic or related to more general loading rather than specifically to knuckle walking behavior.

As with phalanges, differences in NCMA curvature across taxa are more pronounced than differences in IA, with bonobos and *P. t. schweinfurthii* tending to have higher values than the other two taxa. If lower NCMA (relatively greater bending strength) is related to increased knuckle walking, this may relate to overall frequencies of terrestrial behavior, which may be higher in these taxa than in *P. t. verus*. NCMA also increases with age, as would be predicted from increases in knuckle walking behavior, although this change occurs in both metacarpals and metatarsals, suggesting that knuckle walking may not be the only causative factor and that other variables such as overall increases in body size or differences in the loading environment of the hands and feet may also be playing a part (Section 4.1.2.3; Figure 4.6).

Thus, variation in curvature measurements both across adults and during ontogeny generally are in accordance with predictions based on behavior. The overall similarity in developmental patterns between metacarpals and metatarsals, despite different biomechanical pressures, seems to suggest greater genetic effects on the development of these characteristics than formerly suggested. Additionally, the fact that metacarpal Zx was used as the denominator for calculating phalangeal NCMA may be biasing results. Future work should include measures of true phalangeal cross-sectional geometry. This study also did not explicitly consider the effects of hand posture variation either in adults or during ontogeny (Inouye, 1989; 1994b; a), which could conceivably

have a substantial impact on hand bone cross-sectional geometry. Further work is necessary to address these issues.

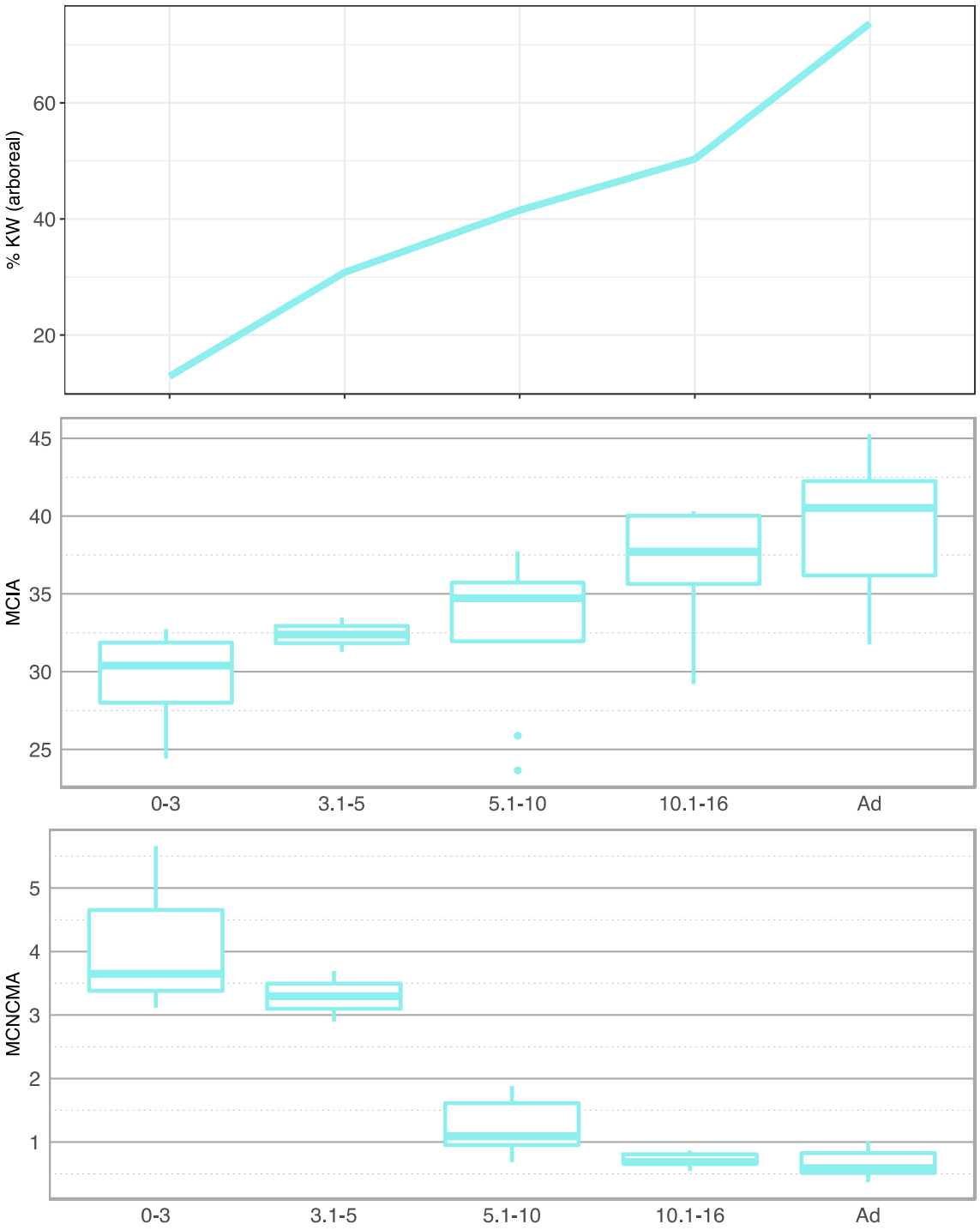

Figure 4.6 Knuckle walking, Metacarpal NCMA, and Metacarpal IA in P. t. schweinfurthii *age classes (Knuckle walking data from Sarringhaus (2013a)*

4.2 METACARPAL AND METATARSAL HEAD MORPHOLOGY

This section presents an analysis of metacarpal and metatarsal dorsal ridge height. As in the analyses of joint dimensions in the previous chapter, these variables are not consistently measurable throughout ontogeny, so analyses in this section proceed as those in Section 3.3: namely, while analyses for adults follow the same protocol as in other sections, ontogenetic analyses take place on raw values grouped into Old Infant, Juvenile, and Adolescent age bins, with Wilcox rank-sum tests (single or pairwise, depending on taxonomic level of analysis), used to test for taxon differences.

Table 4.8 Dorsal ridge variables

Variable	Abbreviation
Presence/Absence	
3rd Metacarpal ridge presence	--
3rd Metatarsal ridge presence	--
Dorsal Ridge Height	
Metacarpal ridge height	MCDMR
Metatarsal ridge height*	MTDMR
Dorsal Ridge Angle	
3rd Metacarpal ridge angle*	MCAngle
3rd Metatarsal ridge angle	MTAngle

**not normally distributed; see text for details of analysis*

Variables analyzed in this section are presented in Table 4.8 and include several different measurements of dorsal ridge height. Analyses began with simple presence/absence (with ridge "presence" defined as having an angle between the point at the tip, base of the ridge, and line tangent to the articular surface of less than 180 degrees). Two measurements were used to quantify ridge development: first, the ridge height measured perpendicular to the line tangent to the articular surface (Inouye and Shea, 2004), and second, the angle used to define ridge presence, which has been

suggested to better correlate with behavior (Sarringhaus, 2013a). Ridge height was only measured on individuals with ridges that are present (i.e., with ridge angle of less than 180 degrees), while analyses of ridge angle include all individuals in which it was measured, including individuals for which the ridge was ultimately defined as absent. Because one is partially a function of the other, in general, larger ridge angles are associated with smaller dorsal ridge heights, but there is some scatter in this relationship, making it worthwhile to examine each separately (Figure 4.7). All variables were analyzed unlogged because this maximized normality.

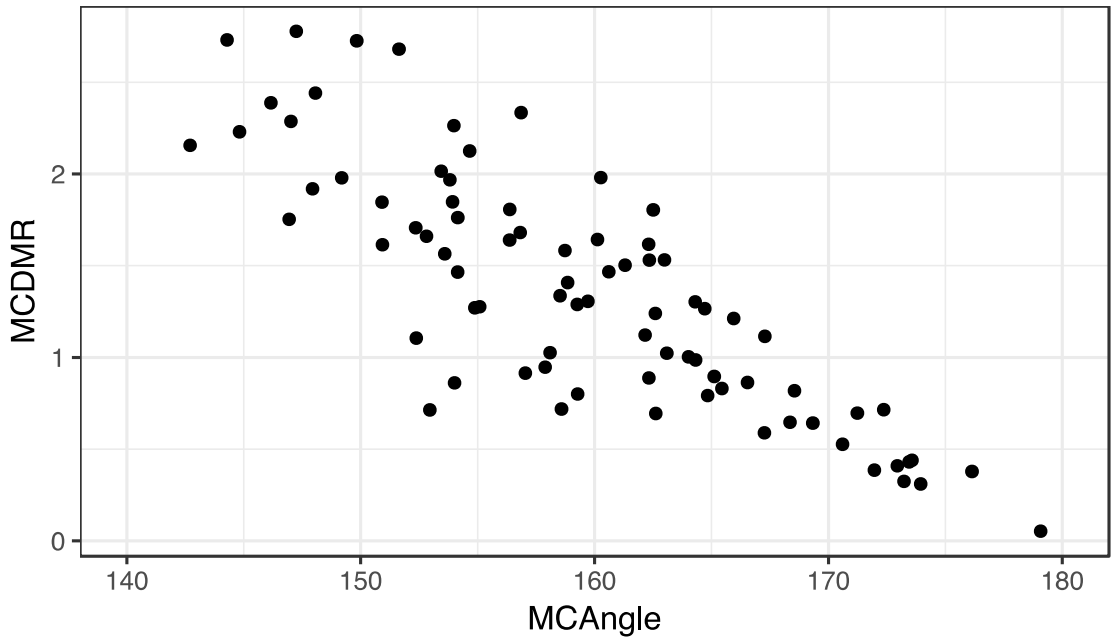

Figure 4.7 3rd Metacarpal dorsal ridge height and angle in Pan *adults with ridges present (3rd metatarsal not depicted, but shows similar relationship)*

4.2.1 Adults

4.1.1.1 Species-level analyses

Table 4.9 and Table 4.10 present measurements of ridge presence/absence, heights, and angles by sex in *P. paniscus* and *P. troglodytes*. Note that sample sizes for

ridge angles always outnumber sample sizes for ridge heights, because height is only measured on dorsal ridges that are defined as present. For presence/absence, Fisher's Exact tests were used to test for differences in ridge presence between sexes within species; for continuous variables, two sample t-tests with unequal variance or Mann-Whitney U tests with Bonferroni-corrected significance levels were used ($\alpha < .05/2$). No variables were significantly different between sexes, so sexes were pooled for further analyses.

Table 4.9 Counts for and sex differences in dorsal ridge presence/absence in adults (species)

	P. paniscus				***P. troglodytes***			
	Male		**Female**		**Male**		**Female**	
	Present	**Absent**	**Present**	**Absent**	**Present**	**Absent**	**Present**	**Absent**
Metacarpal	6	1	10	0	24	4	36	0
Metatarsal	6	1	4	6	13	14	15	22

The majority of adult specimens measured in both *P. paniscus* and *P. troglodytes* tend to have dorsal metacarpal ridges present, but the pattern is different in dorsal metatarsal ridges, which are more evenly split in male *P. troglodytes* and absent in about 60% of female *P. paniscus* and *P. troglodytes* (male *P. paniscus* show similar frequencies between the two bones but also have the smallest sample sizes; Table 4.9). Where dorsal ridges were present, species differences in heights were tested with two sample t-tests with unequal variance or Mann-Whitney U tests. In the metacarpal, bonobos have significantly smaller DMR heights and larger DMR angles than *P. troglodytes*, but no such differences exist in the metatarsal (Figure 4.8). From these plots, it is also clear that within species, dorsal ridges are shorter and angles are less steep for the metatarsals than the metacarpals.

Table 4.10 Summary statistics for and sex differences in dorsal ridge height and angle in adults (species)

	P. paniscus						***P. troglodytes***					
	Male			**Female**			**Male**			**Female**		
Variable	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**
MCDMR	7	0.74	0.34	10	0.89	0.39	24	1.59	0.64	36	1.46	0.61
MTDMR*	1	0.62	NA	4	0.21	0.27	13	0.46	0.36	15	0.33	0.25
MCAngle	7	170.0	9.0	10	165.8	5.8	28	161.4	12.7	36	157.4	8.4
MTAngle	6	184.5	9.4	10	179.8	7.8	27	180.5	8.8	37	180.4	7.7

Bold values are significantly different between males and females within species
**Not analyzed in P. paniscus because of sample size*

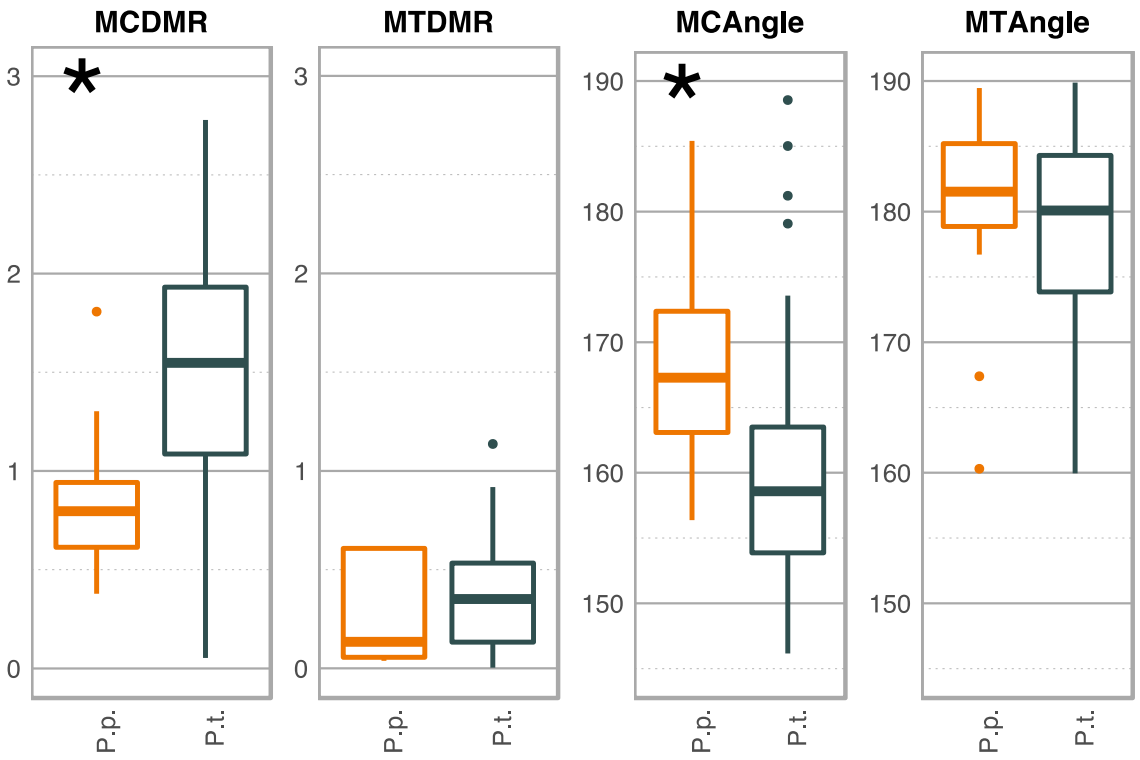

Figure 4.8 Boxplots of DMR in P. paniscus (P.p.) and P. troglodytes (P.t.). Significant differences are indicated with asterisks. Note that DMR angles above 180 degrees are "absent" and thus do not have measured DMR heights.

4.1.1.2 Subspecies-level analyses

Where sample sizes were large enough to test for sex differences, males and females were not significantly different in ridge presence, height, or angle (assessed by Chi-squared tests or two sample t-tests with unequal variance/Mann-Whitney U tests, respectively, as in previous sections; Table 4.11, Table 4.12). Sexes were therefore pooled for analysis of subspecies differences.

Again, the majority of adults, regardless of sex, have "present" DMRs on their metacarpals—in fact, the DMR is only absent in four specimens (all male *P. t. troglodytes*; Table 4.11). This is not true for MT DMRs, which are more evenly split. Ridge angles (for all specimens) and ridge heights (for those with "present" DMRs) were analyzed using two sample t-tests with unequal variance or Mann-Whitney U tests, as in previous sections. There is evidence for subspecies differences in both metacarpal heights and angles, but not in the metatarsal. *Post hoc* tests (Games-Howell tests at a family-wise error rate of .05) find significantly larger metacarpal ridges in *P. t. troglodytes* and *P. t. verus* than in *P. paniscus* (Figure 4.9). The pattern of generally lower DMR ridges in *P. paniscus* than in these two subspecies, with *P. t. schweinfurthii* closer to other *P. troglodytes* but not significantly different from either, persists even when DMR height is scaled by body mass (although only *P. t. verus* differs significantly from *P. paniscus* in this once body mass is factored in), suggesting that size may not be the sole driver of this feature (Figure 4.10).

Table 4.11 Counts for and sex differences in dorsal ridge presence/absence in adults (subspecies)

	P. t. schwein.				***P. t. trog.***				***P. t. verus***			
	Male		**Female**		**Male**		**Female**		**Male**		**Female**	
	Present	**Absent**	**Present**	**Absent**	**Present**	**Absent**	**Present**	**Absent**	**Present**	**Absent**	**Present**	**Absent**
Metacarpal	2	0	6	0	14	4	19	0	8	0	11	0
Metatarsal	1	1	3	3	8	10	6	13	4	3	6	6

Table 4.12 Summary statistics for and sex differences in dorsal ridge height and angle in adults (subspecies)

	P. t. schwein.						***P. t. trog.***						***P. t. verus***					
	Male			**Female**			**Male**			**Female**			**Male**			**Female**		
Variable	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**
MCDMR	2	1.83	0.27	6	1.38	0.60	14	1.48	0.54	19	1.51	0.62	8	1.73	0.86	11	1.41	0.65
MTDMR*	1	0.17	NA	3	0.36	0.15	8	0.63	0.33	6	0.34	0.19	4	0.19	0.24	6	0.31	0.36
MCAngle	2	154.9	2.1	6	154.2	9.6	18	165.2	13.1	19	159.1	6.8	8	154.7	10.3	11	156.3	10.1
MTAngle	2	184.0	11.2	6	177.3	8.0	18	179.6	9.3	19	181.5	6.2	7	182.0	8.0	12	180.1	9.6

Bold values are significantly different between males and females within subspecies
** not analyzed in P. t. schweinfurthii because of sample size*

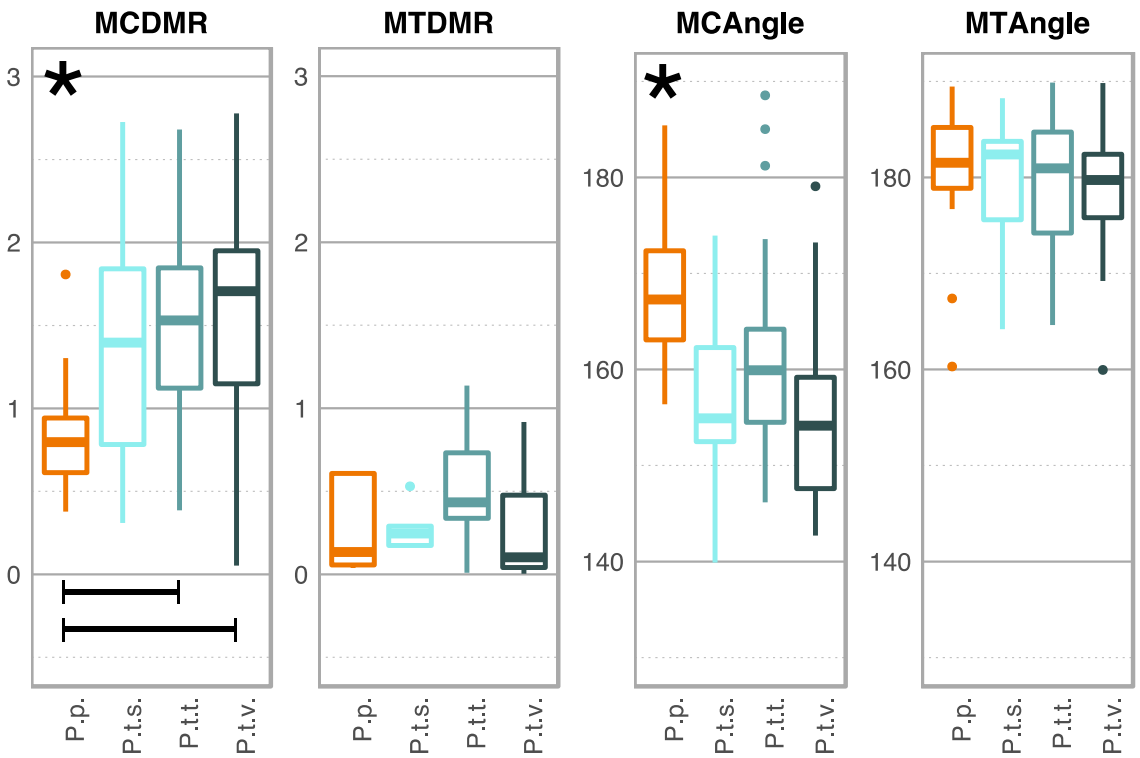

Figure 4.9 Boxplots of DMR in P. paniscus *(P.p.) and* P. t. schweinfurthii *(P.t.s.*), P. t. troglodytes *(P.t.t.), and* P. t. verus *(P.t.v.). Significant differences are indicated with asterisks and significant post hoc tests with bars. Note that DMR angles above 180 degrees are "absent" and thus do not have measured DMR heights.*

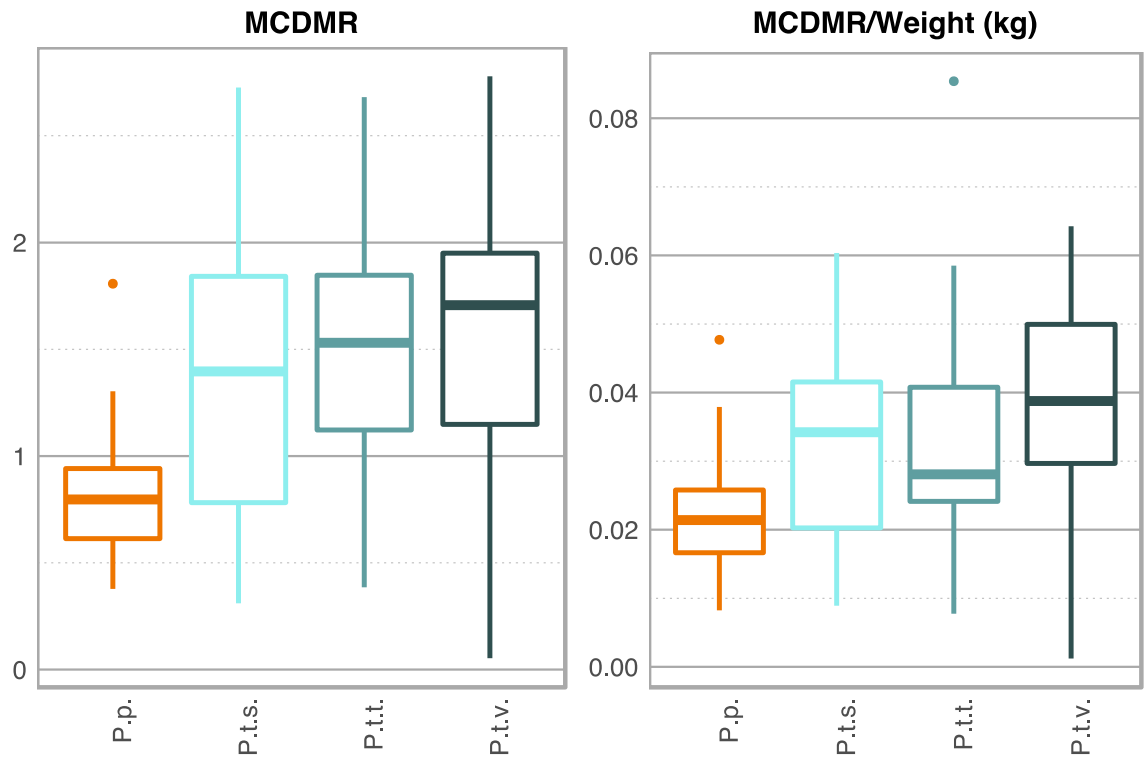

Figure 4.10 Comparison of raw and scaled MC DMR height (MT not shown). Taxonomic abbreviations same as previous figure; significant post hoc differences between P. paniscus *and* P. t. troglodytes/verus *in raw MC DMR and between* P. paniscus *and* P. t. verus *in scaled MC DMR.*

4.2.1.3 Summary

There are no sex differences in DMR presence or angle, or in DMR height where the ridge is present, at either the species or the subspecies level. Regardless of taxon or sex, most individuals in the study had dorsal ridges on their metacarpals, but ridges were more variably present on the metatarsal. Dorsal ridges tend to be shorter and angles less steep on metatarsals then they are on metacarpals. There are no taxonomic differences in either measurement in metatarsals, but bonobos have smaller metacarpal heights and less steep DMR angles than *P. t troglodytes* as a whole, and smaller DMR heights than *P. t.*

troglodytes and *P. t. verus* (although angles were not significantly different). This effect is present, although less pronounced, even when scaled by body mass.

4.2.2 Ontogenetic

4.2.2.1 Species-level analyses

No individuals in the Young Infant age group had measurable metacarpal or metatarsal DMRs, and only two individuals had measurable DMRs in the Old Infant age group (Table 4.14). In Juveniles, although four *P. paniscus* had metatarsal heads where angles were measureable, none of these had DMRs that were present according to the study criteria and so none have DMR heights. For these measurements in these groups, although data are presented, no statistical analyses were performed. For presence/absence (Table 4.13), because many of the expected values under the null hypothesis are less than 5, Fisher's Exact tests are used instead of the chi-squared tests employed in adult analyses. Mean heights increases with age within species and mean angles decrease, but there are no significant differences between species within any age group (Table 4.14).

4.2.2.2 Subspecies-level analyses

Differences between bonobos and the three common chimpanzee subspecies in each age group were tested with pairwise Wilcox rank-sum differences (alpha = .05).

Table 4.13 DMR presence/absence in age bins/species

	P. paniscus						***P. troglodytes***					
	Old inf		**Juv**		**Adol**		**Old inf**		**Juv**		**Adol**	
	Present	**Absent**	**Present**	**Absent**	**Present**	**Absent**	**Present**	**Absent**	**Present**	**Absent**	**Present**	**Absent**
Metacarpal	0	1	5	1	8	0	1	1	17	6	16	0
Metatarsal	1	0	0	4	4	2	0	2	5	17	5	8

Table 4.14 DMR height and angle in age bins/species

	Old Inf. (2-5y)				**Juv. (5-10y)**				**Adol. (10-14y)**			
	P. pan.		***P. trog.***		***P. pan.***		***P. trog.***		***P. pan.***		***P. trog.***	
Variable	*n*	*mean(SD)*	*n*	*mean(SD)*	*n*	*mean(SD)*	*n*	*mean(SD)*	*n*	*mean(SD)*	*n*	*mean(SD)*
MCDMR	0	NA	1	0.34(NA)	5	0.37(0.40)	17	0.65(0.42)	8	0.99(0.47)	16	1.29(0.62)
MTDMR	1	0.76(NA)	0	NA	0	NA	5	0.36(0.34)	4	0.44(0.41)	5	0.21(0.14)
MCAngle	1	186.1(NA)	2	182.1(13.7)	6	174.6(6.6)	23	172.2(9.8)	8	166.3(6.4)	16	159.5(8.0)
MTAngle	1	165.2(NA)	2	193.6(3.7)	4	187.8(3.1)	22	185.7(9.8)	6	175.4(9.1)	13	185.7(10.0)

Table 4.15 DMR presence/absence in age bins/subspecies

	P. t. schweinfurthii						***P. t. troglodytes***						***P. t. verus***					
	Old inf		**Juv**		**Adol**		**Old inf**		**Juv**		**Adol**		**Old inf**		**Juv**		**Adol**	
	P	**A**	**P**	**A**	**P**	**A**	**P**	**A**	**P**	**A**	**P**	**A**	**P**	**A**	**P**	**A**	**P**	**A**
Metacarpal	--	--	5	0	14	0	1	1	11	4	6	0	--	--	2	0	5	0
Metatarsal	--	--	1	5	1	3	0	2	4	12	4	1	--	--	--	--	0	4

Breaking *P. troglodytes* results for DMR presence/absence down into subspecies (Table 4.15) shows that substantially more data are available for *P. t. troglodytes* than for the other subspecies, especially for the Old Infant age group, which is represented entirely by *P. t. troglodytes*. Overall, the proportions of metacarpal DMRs that are "present" according to the study criteria increase with age, but this trend is less apparent in the metatarsal (although data are too sparse to allow for confident interpretation).

Summary statistics and sample sizes for DMR height and angle in each age group are reported in the Supplementary Information. Sample sizes were too small for statistical analysis in the Old Infant age group and in metacarpal DMR height for the Juvenile age group, but these are still represented visually along with other age/taxon group data in Figure 4.11. In all other instances, if a single taxon was missing data, it was excluded from analysis and pairwise comparisons were performed between the remaining groups. Although no differences within groups are significant, the metacarpal shows a clear pattern of increase in DMR height and decrease in DMR angle with age (Figure 4.11). No corresponding trend is seen in the metatarsal. DMR heights relative to body mass show less change with age, while adults still have relatively lower DMR angles relative to body mass compared to infants (Figure 4.12). The extent to which these results are impacted by ontogenetic change in the joint cartilage is unclear.

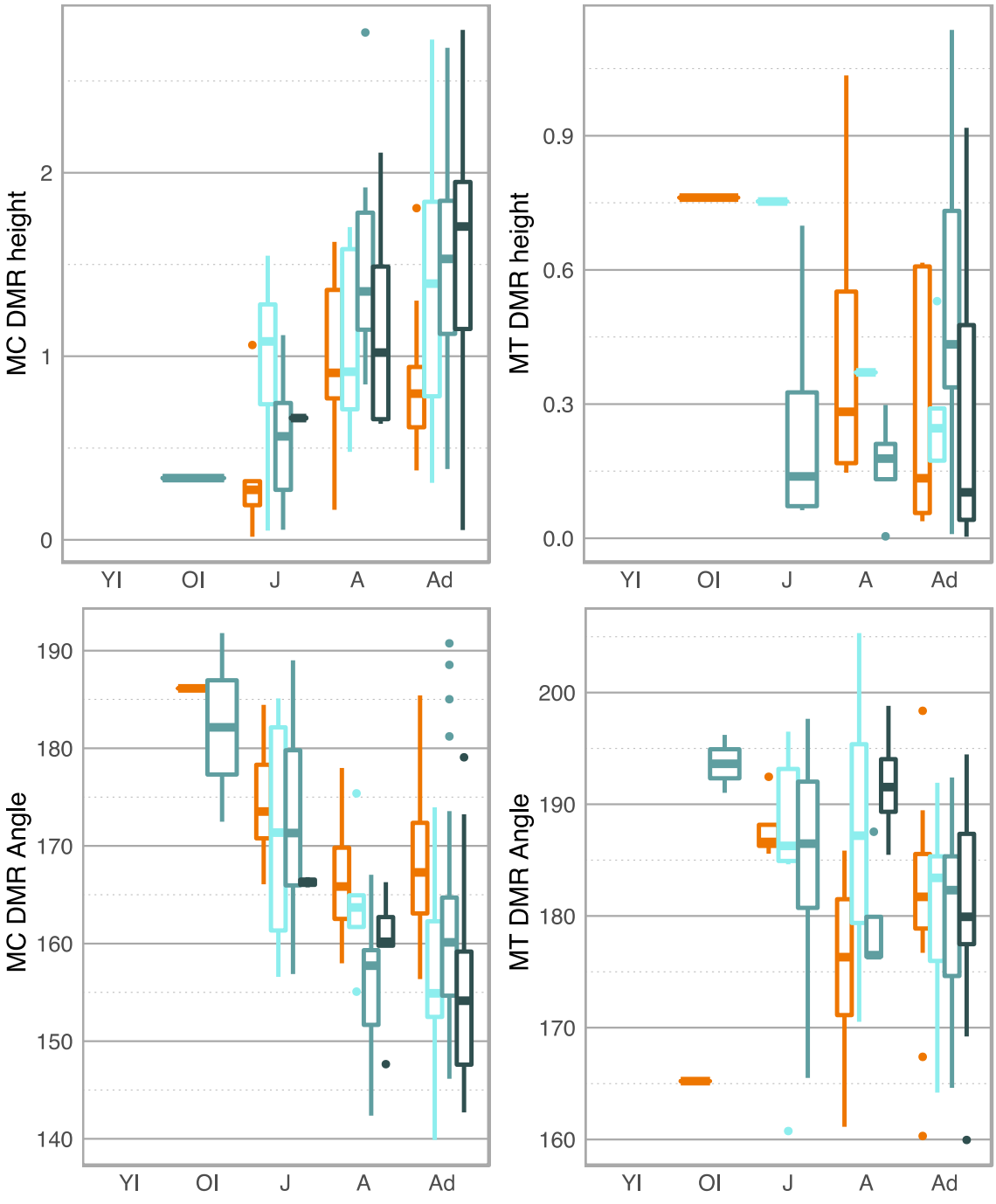

Figure 4.11 DMR height and angle in P. paniscus *and* P. troglodytes *subspecies/age groups.*

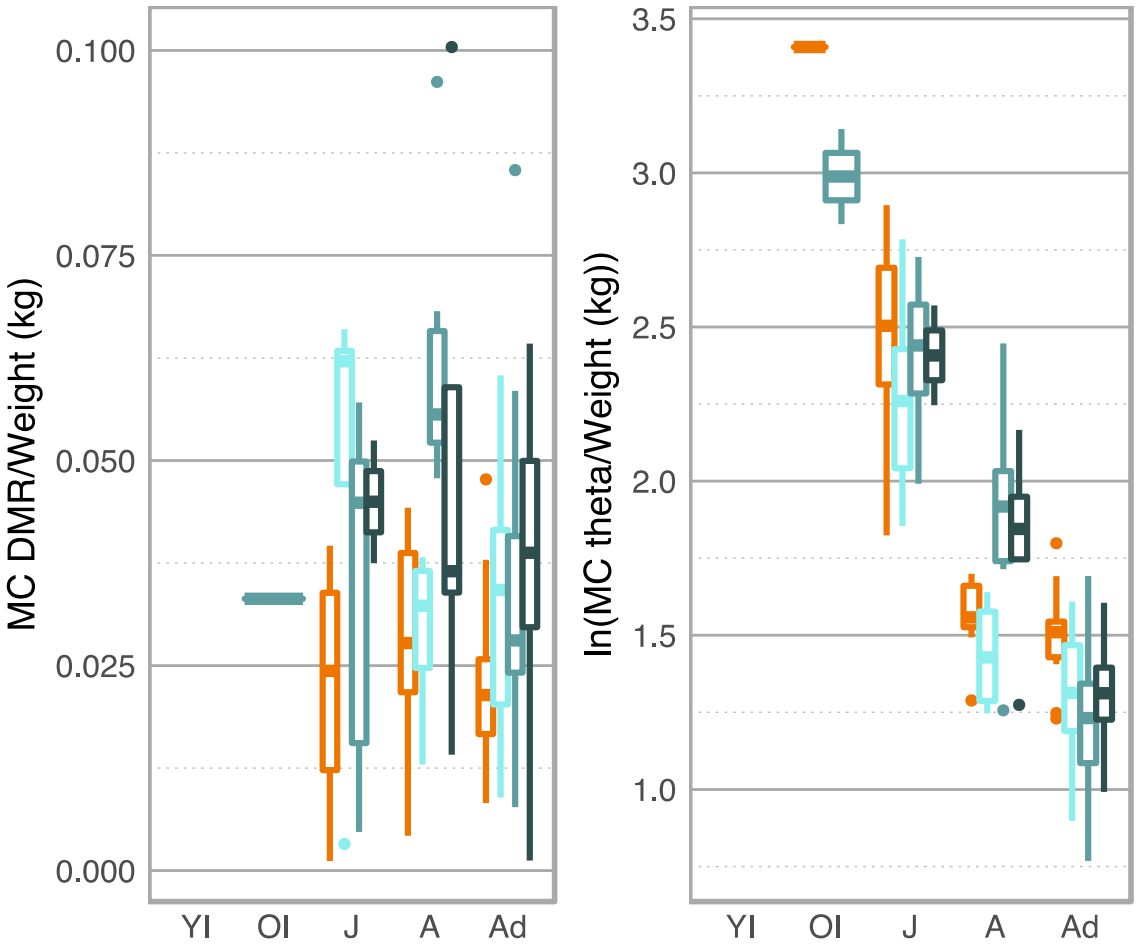

Figure 4.12 Metacarpal DMR angle and height scaled by body mass (metatarsal not shown)

4.2.3 Comparison to behavioral data

DMR height and presence has often been discussed as a knuckle walking-related feature, but previous studies have not always found unequivocal links. Instead, DMR height and presence has been suggested to relate to knuckle walking behavior only secondarily, primarily existing as a response to body size (Inouye and Shea, 2004), although DMR angle may be more directly behaviorally mediated (Sarringhaus et al., 2013). Regardless, it is difficult to explain in the context of knuckle walking why a DMR would be found on the metatarsals. As discussed in the previous section, data on differences in frequencies of knuckle-walking behavior among adults are sparse, but

quantitative and qualitative ontogenetic locomotor data both indicate increases in knuckle walking behavior with age.

Overall, there is more variation between taxa and age groups in DMR height in the metacarpals than in metatarsals, which is consistent with some kind of link to hand postures used in quadrupedal locomotion, either primarily or secondarily through body size (as foot postures remain similar regardless of the type of quadrupedalism used). In general, there were more differences in DMR height than there were in DMR angle in adults, with bonobos having generally shorter heights and larger angles even when body mass was factored in. At the subspecies level, however, only DMR heights differed between *P. paniscus* and *P. t. troglodytes* and *P. t. verus*. When analyzed directly, both DMR height and angle are correlated with body size in the entire sample; within subspecies these correlations are only significant at a family-wise significance level of .05 in *P. troglodytes*, which may primarily be due to sample size (Table 4.16). These results are difficult to interpret in light of the behavioral data available. Both variables seem to be related in some way to body size at least on a broad level, but the fact that taxonomic differences persist even when heights and angles are scaled by body mass (Figure 4.12) also suggests additional possibly behavioral effects.

Table 4.16 Correlations between DMR measurements and body mass

	R Squared*			
Taxon	**MCDMR**	**MTDMR**	**MCAngle**	**MTAngle**
Pan	**0.48**	0.06	**-0.38**	-0.12
P. paniscus	0.39	-0.17	-0.38	0.05
P. troglodytes	**0.47**	0.12	**-0.36**	-0.16
P. t. schweinfurthii	0.50	-0.56	-0.42	-0.04
P. t. troglodytes	**0.52**	0.39	**-0.38**	-0.20
P. t. verus	0.38	-0.56	-0.29	-0.28

** Bold = significant at .05*

4.3 SUMMARY

In summary, both curvature and dorsal ridge height are sometimes in accordance with predictions from their hypothesized relationships with behavior, but do not always follow predictions. Interpretation is complicated by behavioral and morphological variation within taxa and by the incompleteness of available behavioral data. Further study will be necessary to clarify the nature of the relationships to behavior suggested by the data presented in this chapter and by previous work.

5 DISCUSSION AND CONCLUSIONS

This chapter reviews and contextualizes the findings of the previous chapters in reference to the hypotheses and predictions laid out in Chapter 1. This discussion is followed by a summary of the conclusions and broader implications of the study.

5.2 DISCUSSION

5.1.1 Hypotheses 1 and 2

5.1.1.1 Lengths, articular surfaces, and geometric properties

It was hypothesized that bone lengths, articular proportions, cross-sectional geometry, and external curvature are not equally sensitive to behavioral variation during an individual's lifetime, with length ratios and articular proportions inferred to be primarily genetically controlled (Hypothesis 1) and cross-sectional geometry and curvature more influenced by the loading environment (Hypothesis 2). Under these hypotheses, bone length and articular surface ratios were predicted to primarily vary along phylogenetic lines, with more differences between *P. paniscus* and *P. troglodytes* subspecies than among *P. troglodytes* subspecies, and these patterns of differences were predicted to appear early in development and remain through adulthood. In contrast, cross-sectional geometry and phalangeal curvature were predicted to follow behavioral lines both within and across taxa – specifically that higher phalangeal curvature and relatively stronger forelimb bones should be associated with greater amounts of arboreal behavior, both across species and subspecies as adults and within the ontogeny of each individual taxon. Based on available behavioral data, it was predicted that values for both types of characteristics should be highest (and most similar between taxa) in infancy and

diverge later as behavioral repertoires also diverged. It was also noted that ontogenetic patterning of these values has a bearing on the concept of adult *P. paniscus* as "locomotor paedomorphs" based on previous behavioral data. Similarity in these hypothesized behavioral indicators between adult bonobos and immature common chimpanzees would support this proposed locomotor paedomorphism in *P. paniscus*, while greater similarities between adults of the two taxa would not, instead supporting similarity in adult locomotor repertoires (as suggested by recent behavioral data).

As predicted based on Hypothesis 1, the majority of significant differences in limb and articular proportion ratios were found between *P. paniscus* and *P. troglodytes* and were apparent from early in development, although small sample sizes limited the potential for interpreting trends early in infancy. Some other significant differences were found at various ontogenetic stages, but were transient and did not show significant patterns (potentially also due to sample size). In many instances, traits that differentiated bonobos and common chimpanzees as a group failed to reach significance when compared between bonobos and the three subspecies separately. There were only a handful of significant differences between subspecies of *P. troglodytes*, either as adults or during ontogeny – the vast majority of differences found were between *P. paniscus* and *P. troglodytes* or individual *P. troglodytes* subspecies.

In bone lengths, the clearest patterns were found in femur/humerus length, overall hind limb/forelimb length, and metatarsal/metacarpal length ratios, which in adults were all higher in *P. paniscus* than in *P. troglodytes* and, in the case of femur/humerus length, than all *P. troglodytes* subspecies individually as well. Differences in the femur/humerus ratio appear to be present in immature individuals as well, but do not reach significance

until the juvenile (for *P. paniscus* vs. *P. troglodytes*) or adolescent (*P. paniscus* and *P. troglodytes* subspecies) age groups. In contrast, metatarsal/metacarpal length ratios are similar in immature individuals for all taxa. Joint ratios are even more similar across taxa: the most consistent difference is found in the relative size of the humeral head, which is smaller compared to both the femoral head and the distal humerus in *P. paniscus* than it is in *P. troglodytes* (including *P. troglodytes* subspecies) in adults. (It is noted that this ratio could not be measured through the entire ontogenetic trajectory because of the nature of the formation of epiphyses). These patterns do not correlate with behavior; morphological differences are not found between *P. troglodytes* subspecies despite clear differences in behavioral patterns.

The patterns of limb length differences found in the current study are slightly different from those discussed in previous large summaries of morphological differences in *Pan,* such as Jungers and Susman (1984). Most notably, significant differences between adult *P. t. schweinfurthii* and *P. paniscus* in total hind/fore limb lengths were not found in the current study. This could be for a number of methodological or statistical reasons. Results from different studies comparing the morphology of chimpanzees and bonobos at these taxonomic levels often seem to slightly contradict each other (see Zihlman, 1978; McHenry, 1981; Morbeck and Zihlman, 1989), perhaps because the true differences between taxa may actually be relatively slight, meaning that sample composition and sample size have relatively large effects.

The lack of significant difference between *P. troglodytes* subspecies in intermembral index (IMI) found in previous studies is not consistent with the more general relationship between IMI and body size in African apes, in which larger body

size tends to be associated with longer forelimbs (Cartmill, 1974; Jungers and Susman, 1984). This effect has been hypothesized to be at least partially explained by the mechanics of climbing on large vertical substrates, in that at larger body sizes, longer upper limbs make climbing more efficient by allowing the individual to augment pedal friction by leaning backwards (Cartmill, 1974). The lack of significant difference between adult *P. paniscus* and *P. t. schweinfurthii* found in the current study (and their relatively shorter forelimbs compared to hind limbs) is actually more consistent with this hypothesis, as these two taxa have smaller adult body sizes than the other two *P. troglodytes* subspecies. (As discussed in the Introduction, body mass data for *P. t. verus* are sparse, but suggest that they are slightly larger than *P. t. schweinfurthii,* although more similar in size to *P. t. schweinfurthii* than to *P. t. troglodytes.*) This interpretation is also supported by the fact that in the whole sample of adults, as in the total ontogenetic sample, intermembral index increases with body size (Figure 5.1, Figure 5.2). Actual body mass data, as opposed to body mass estimated from skeletal dimensions, would be helpful in further exploring these trends.

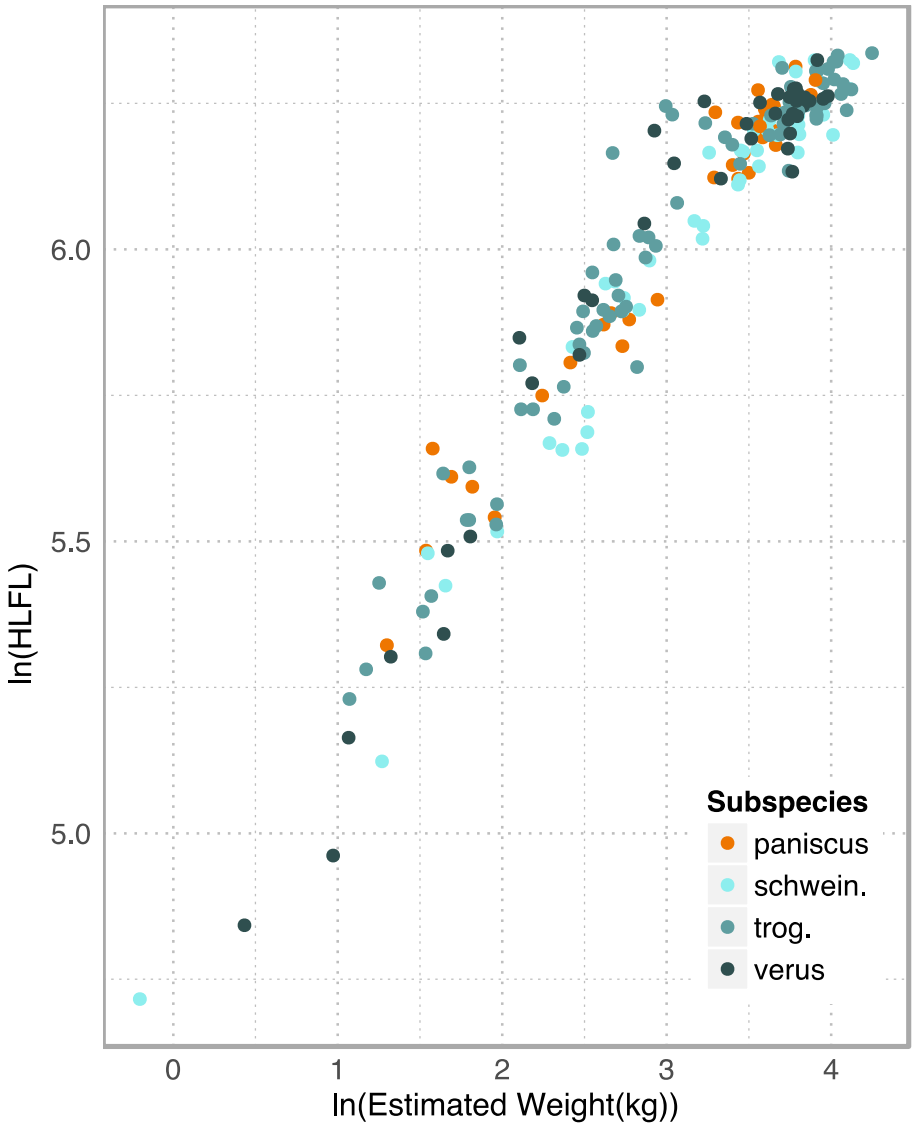

Figure 5.1 Ontogenetic scaling of hind limb/forelimb length (HLFL) and estimated body mass in Pan

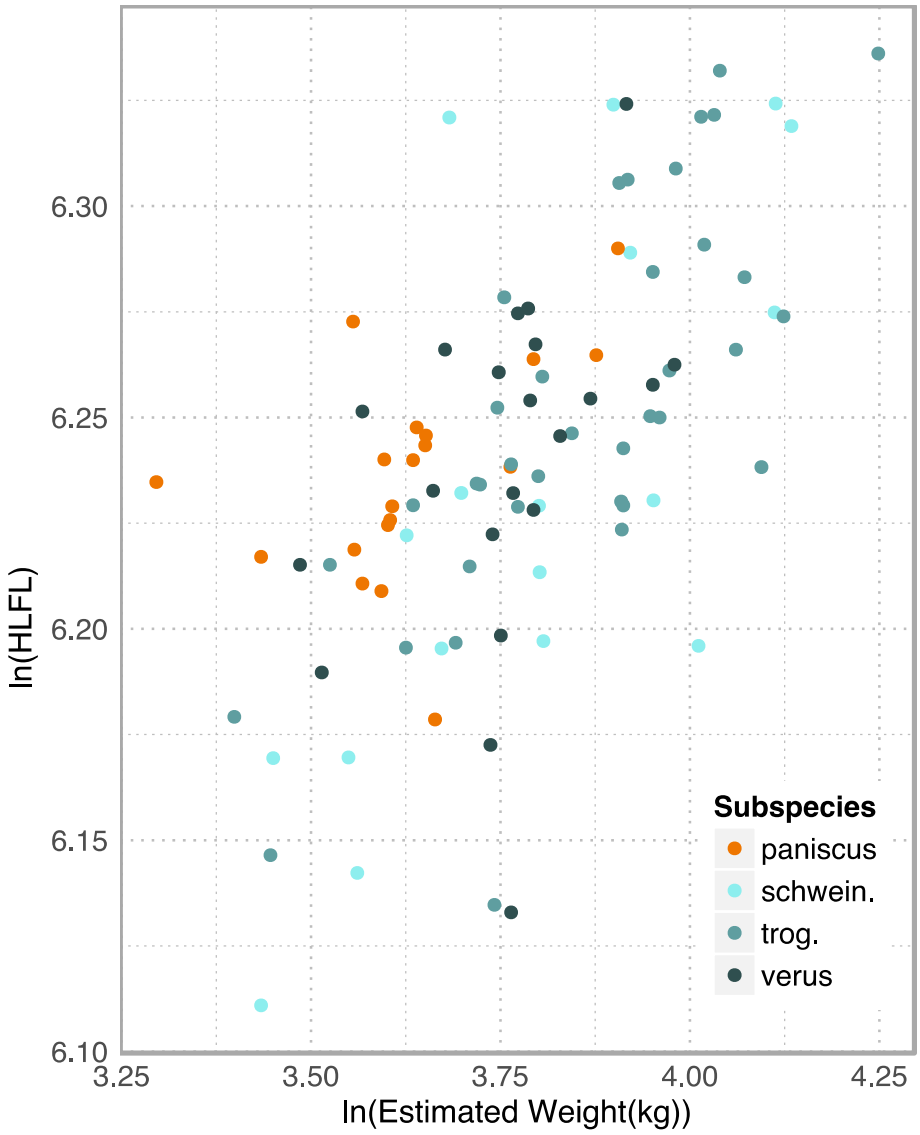

Figure 5.2 Hind limb/forelimb length (HLFL) and estimated body mass in adult Pan

Hypothesis 2 was also mostly supported: strength proportions seemed to track frequencies of arboreal behavior both within and across subspecies and species, with more instances of significant differences within *P. troglodytes* than were present in articular and length parameters. In adults, *P. t. verus* and *P. t. troglodytes* have relatively lower femur/humerus strength ratios, with *P. t. schweinfurthii* intermediate between them and *P. paniscus*, and not different from any of them. This tracks behavioral data fairly

well, in which adult *P. t. verus* have higher frequencies of climbing and *P. t. schweinfurthii*, at least those from Gombe and Mahale, are more similar to *P. paniscus*. Trends in femoral circularity also matched predictions based on behavior, with more A-P strengthened femora found in the more quadrupedal taxa. Ontogenetically, hind- to forelimb strength ratios also matched predictions, increasing with age in all taxa and showing greater similarity in infancy than in older age groups, which is in accordance with a greater impact of the individuals' behavior during development on these aspects of their morphology. However, not all patterns were completely consistent with predictions. There are some differences in fore- and hindlimb loading behaviors between *P. paniscus* and *P. t. schweinfurthii*, especially in females, that do not seem to be reflected in morphology (see Figure 3.13). Also, in some non-adult age cohorts *P. t. verus* have more extreme values of femoral shape than would be expected based on behavior, with behavior suggesting that they should have the most circular bones at all ages.

These findings add to the large, and growing, body of literature supporting the distinction between these two types of morphological characteristics. Many of these previous studies have examined patterns of variation across relatively broad taxonomic scales in adults and have found that the relative strength of the fore- to hind limb bones distinguishes broad locomotor categories (Schaffler et al., 1985; Demes and Jungers, 1993; Ruff, 2002; Habib and Ruff, 2008). While important to our understanding of bone biology, these results are of limited practical utility in interpreting fossils, especially in the hominin and Miocene hominoid radiations, which are made up of many closely-related forms that seem to exhibit more subtle and often mosaic locomotor adaptations (Fleagle, 2013). Accordingly, as summarized in the Introduction, recent studies have

increasingly focused on changes in the locomotor skeleton over relatively small amounts of evolutionary time and narrower behavioral differences. These studies often use ontogeny as a means of controlling for genetic impact, but some have also used fluctuating asymmetry as a means of testing for developmental stability (e..g, Reeves et al., 2016).

In African apes, these patterns have been documented in mountain and lowland gorillas, which initially diverged over 1 million years ago, with gene flow until around 20-80,000 years ago (Langergraber et al., 2012). Inter-limb diaphyseal strength proportions and behavior are similar in infants until two years of age, at which time both locomotor behaviors and fore- to hind limb strength proportions diverge, but no similar patterns are seen in length or articular proportions (Ruff et al., 2018). Common chimpanzees and bonobos had an initial divergence probably closer to around 1 million years ago (Won and Hey, 2004; Caswell et al., 2008; Hey, 2010; Wegmann and Excoffier, 2010; Gonder et al., 2011; Langergraber et al., 2012; Prado-Martinez et al., 2013), but *P. troglodytes* subspecies diverged from one another much later and two (*P. t. schweinfurthii* and *P. t. troglodytes*) may not be genetically distinct subspecies at all (Fischer et al., 2006; Gonder et al., 2011; Fünfstück et al., 2015). Members of the genus *Pan* are also are likely more similar to one another in behavior than are mountain and lowland gorillas (Doran, 1989). That bonobos and common chimpanzees *do* exhibit some differences in inter-limb length proportions, but common chimpanzee subspecies do not, suggests that the evolutionary timescale of these subspecies divergences may not have been sufficient for length differences to evolve, but that it is possible for substantial length differences to arise even over the relatively short evolutionary time frame that

separates bonobos from common chimpanzees. (Or alternatively, that there are no selective pressures driving them). The differences in cross-sectional strength proportions between common chimpanzee subspecies discussed above suggest that these are sensitive even to the relatively subtle changes in behavioral frequencies found within these closely related taxa. Interestingly, the femur/humerus, tibia/radius, and metatarsal/metacarpal ratios did not equally differentiate taxa (tibia/radius showed the clearest differences, while metatarsal/metacarpal showed none). This is perhaps unsurprising given that the loading environment for each of these bone pairs is likely different, but suggests that further exploration of these differences within a kinematic context may be a fruitful area of investigation.

A previous study (Sarringhaus and MacLatchy, 2016) used similar methods to compare the ontogeny of behavior and limb bone morphology in *P. t. schweinfurthii.* This study found that femoral/humeral strength ratios increased with age and that the femur (but not the humerus) became more elliptical, concurrent with decreases in arboreal behavior. The results from the current study are consistent with these findings, and further suggest that these patterns hold relatively true for *Pan* in general.

Ontogenetic trajectories in strength proportions do not support the idea that bonobos are locomotor paedomorphs of *P. troglodytes*, i.e., that adults share behavioral characteristics with immature common chimpanzees. This interpretation was initially based on behavioral data of only partially habituated *P. paniscus* (Doran, 1993), but more recent information from an habituated sample has suggested that adult *P. paniscus* and *P. troglodytes* may be more similar to one another in behavior (Ramos, 2014). The fact that adult bonobos do not resemble immature common chimpanzees of any subspecies in

fore- to hindlimb strength proportions supports the latter interpretation, suggesting that locomotor paedomorphism may not be the best explanation for bonobo anatomy.

5.1.1.2 Phalangeal curvature

Inter-taxon and ontogenetic variation in phalangeal curvature also did not entirely follow predictions based on previous studies. It has previously been shown that bonobos have slightly more curved phalanges than common chimpanzees (Susman, 1979; Stern and Susman, 1983; Susman et al., 1984; Stern et al., 1995), which have been interpreted to be related to higher degrees of arboreality. Several key studies have directly linked curvature of the phalanx to arboreal behavior, both through biomechanical modeling (Richmond, 2007) and through correlation of phalangeal curvature with behavioral data. Most notably for the purposes of this study, this prior work showed that phalangeal curvature (as measured by Included Angle) decreases with age in hominoids that become less arboreal with age (Richmond, 1998). Accordingly, phalangeal curvature has been frequently cited as one of the most reliable indicators of arboreal behavior, especially in reference to the fossil record, including some immature fossil hominins (Dominguez-Rodrigo et al., 2015; Kivell et al., 2015).

Based on this, this study predicted that phalangeal curvature would track arboreal behavior fairly closely. As in the previous studies discussed above, although IA curvature was not significantly different within sexes, bonobos did have more curved phalanges than common chimpanzees. However, IA curvature changed less with age than cross-sectional geometry, and was extremely variable across adult *P. t. troglodytes*. We also found differences between curvature measured by IA and curvature measured by NCMA, with the latter more consistent with variation in arboreal behavior both across taxa and

during ontogeny. The degree of variation in *P. t. troglodytes* adults is intriguing, but lack of behavioral data for this subspecies makes it very difficult to interpret. It is possible that phalangeal curvature is in reality strongly linked with arboreality and this taxon shows a much larger degree of behavioral variation than the other subspecies. However, if that were the case, we would expect to see correspondingly large variation in cross-sectional properties, which is not the case. One alternative interpretation is that phalangeal curvature in this taxon is additionally impacted by other behaviors (either locomotor or other activities involving the hands). Until further behavioral information is available, it seems prudent to consider these potential additional impacts when using phalangeal curvature to interpret fossil locomotor patterns.

5.1.2 Hypothesis 3

The third hypothesis was that several aspects of metacarpal morphology are also developmentally plastic, specifically with respect to knuckle-walking behavior, with some more directly influenced by body size than others. It was predicted that more metacarpal curvature would be associated with more knuckle-walking behavior (as curvature increases the predictability of loads), both across adults and within the ontogeny of each taxon, but that metatarsal curvature would not necessarily show the same patterns. Dorsal metacarpal ridge height was expected to correlate with body size, as previous studies have suggested that size is the primary mediator of this feature (Inouye and Shea, 2004), while dorsal metacarpal ridge angle was expected to track knuckle walking more directly, again based on previous studies (Sarringhaus, 2013a). Ridge angles and heights on the metatarsals were again not predicted to be as strongly

linked with behavior, as their loading environment should not differ as much (if at all) between knuckle walking and other types of quadrupedal locomotion.

As in phalanges, metacarpal and metatarsal curvature was measured in two ways: included angle (IA), and normalized curvature moment arm (NCMA). The two measurements followed different patterns and did not track each other. Curvature measured by NCMA generally varied in accordance with behavioral predictions based on the available data on knuckle walking frequencies, showing more differences across taxa and during ontogeny, while curvature measured by IA showed no differences across adults, although curvature did increase with age as predicted. Metacarpal and metatarsal curvature also showed more similarity than might be expected given their presumably differing loading environments – for example, both became more curved with age at fairly similar rates. This may in part be due to measurement techniques: because the endpoints were located at the midpoints of articular surfaces to allow for easier comparison to previous studies, changes in the dimensions of the epiphyses may have had an outsized effect on the overall measured "curvature" of the bone. However, it is also possible that these aspects of morphology are more strongly genetically canalized or are responding to more general locomotor pressures that are common to both the hand and foot.

Dorsal metacarpal ridge angle and ridge heights also showed slightly different patterns. DMR angle was less variable across adult *Pan* than DMR height, but both were correlated with body size across adults. When body size was factored in, bonobos still had shorter DMR heights and less steep DMR angles than *P. troglodytes* generally, but only DMR height continued to differentiate them from individual subspecies. Both

therefore seem to relate to body size broadly, but these taxonomic differences even after body mass is accounted for suggest a potential role of behavior as well.

It is notable that *P. paniscus* dorsal metacarpal ridge morphology is different from all *P. troglodytes*, including *P. t. schweinfurthii*, which is similar in body size. This difference has been noted before (Susman, 1979), and explained in the overall context of bonobos generally having more arboreally adapted or "unspecialized" fingers compared to common chimpanzees. However, the fact that new bonobo behavioral data do not suggest that they are more arboreal, as well as the fact that no such systematic differences are seen in the metatarsal, suggests that this may be specifically related to differences in hand posture during locomotion, the most obvious of which would be knuckle walking. As discussed in Chapter 4, data on relative frequencies of different hand postures have not been consistently collected in studies of locomotor behavior in the wild. The most recent studies of bonobos show that about 98% of their locomotion is quadrupedal knuckle walking (Ramos, 2014), while previous studies using only the subset of arboreal behavior showed that both bonobos and *P. t. schweinfurthii* had relatively higher frequencies of arboreal palmigrade quadrupedalism than arboreal knuckle walking. This, combined with the fact that the new data also do not indicate that bonobos are substantially more arboreal than common chimpanzees, suggests that it may not be overall frequencies of knuckle walking behavior that are influencing morphological differences. Rather, it is either possible that there is an unrecognized genetic component to dorsal metacarpal ridge morphology, or that there are more subtle differences in digit or hand posture between bonobos and *P. troglodytes*, perhaps influenced by their overall morphology or posture.

A systematic difference in hand posture between *P. troglodytes* and *P. paniscus* does not seem out of the question. In captivity, bonobos have been observed to adopt a more pronograde trunk posture when knuckle walking, likely because of their longer hind limbs (Susman, 1979). The present study also found systematic differences in intrinsic hand proportions: at least in adults, bonobos have relatively shorter phalanges compared to their metacarpals than *P. troglodytes* and tend to have somewhat absolutely shorter phalanges as well. All else being equal, shorter phalanges should decrease the moment arm of the ground reaction force (Figure 5.3), which could help to explain the DMR ridge height difference regardless of other postural differences.

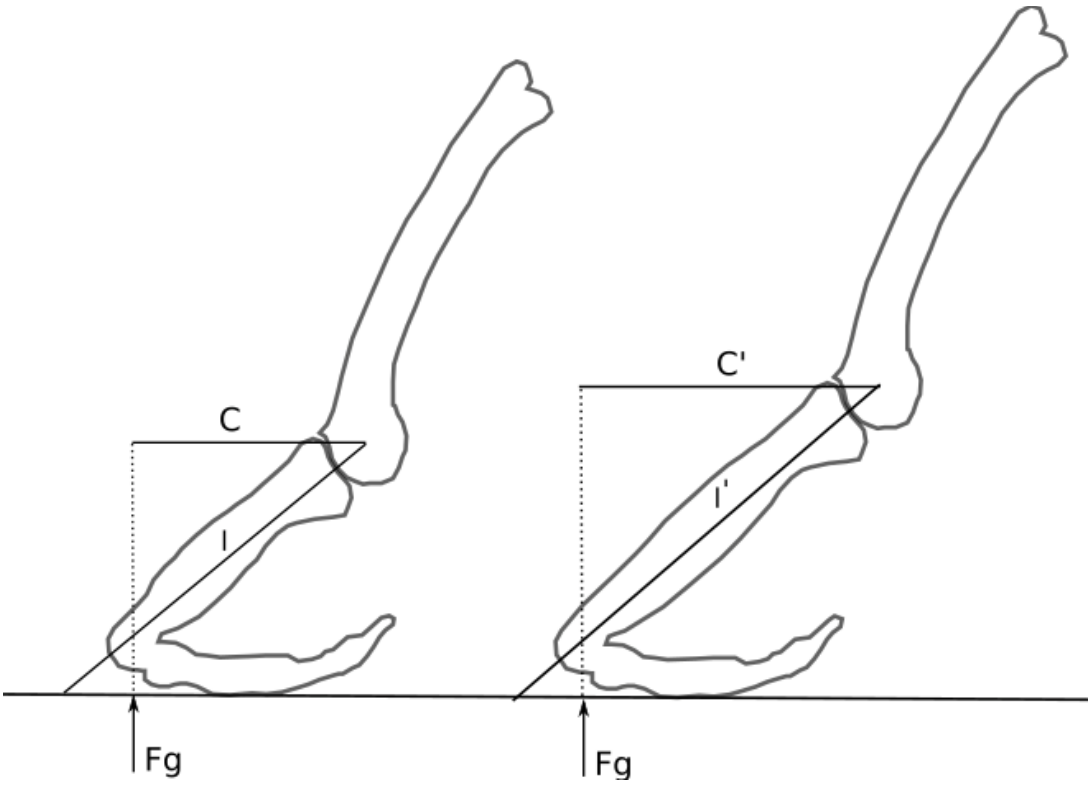

Figure 5.3 Ray III in knuckle walking posture. A longer proximal phalanx increases the moment of Fg (ground reaction force). Figure modified from Susman (1979) Fig. 7.

However, there could also be differences in digit use and hand posture in knuckle walking. Hand posture has been previously hypothesized to impact some aspects of forearm morphology that are behaviorally plastic: in gorillas, ontogenetic changes in hand orientation (i.e., the angle of the palm relative to the direction of travel) have been suggested to influence bone cross-sectional morphology in the radius and ulna of gorillas (Ruff et al., 2013), although there also may be more variation among adult gorillas in hand posture than was previously recognized (Thompson et al, 2018). The 3rd metacarpal is reliably used in knuckle walking in all African apes, including both chimpanzees and bonobos (Inouye, 1994a), so differences in finger use (or lack of finger use) are likely not the driving factor behind 3rd metacarpal head morphology. Studies of hand posture have suggested some differences between *P. paniscus* and *P. troglodytes*: at all sizes, *P. paniscus* prefer angled hand postures (palm angled relative to the direction of travel), while *P. troglodytes* use angled and coronal (palm perpendicular relative to direction of travel) postures about equally, with smaller (younger) chimpanzees more heavily utilizing coronal postures compared to larger, older chimpanzees (Inouye, 1994b). These differences could conceivably have effects on the loading environment of the hand that are not explicitly being taken into account in the current study, especially given that the dorsal metacarpal ridge was only imaged from one side but is in fact a 3D structure that shows some variation from medial to lateral (see Figure 5.4 for example).

Gorilla

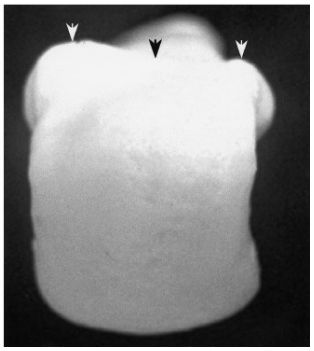

Figure 5.4 Example of mediolateral variation in DMR morphology in Gorilla *(modified from Richmond et al. (2001)*

In general, interpretation of the aspects of hand and foot morphology covered in Hypothesis 3 would benefit from finer-grained information about hand and foot loading and locomotor patterns, both in knuckle walking and in other types of behavior. Because they interact directly with the substrate and are therefore the closest to substrate reaction forces, the hands and feet are often expected to be especially sensitive to hand/foot posture and use (e.g., Tsegai et al. (2013)). Quantitative locomotor data at this level of granularity are difficult or impossible to collect in the wild and were not always available or collected consistently across the behavioral studies referenced for the current analyses, but authors have often discussed these issues, often in the context of the complex interrelationships between body size, locomotion, and the makeup of the arboreal environment. Studies across several different types of primates have demonstrated that individuals at larger body sizes use more climbing and scrambling and less quadrupedalism, as (given the same environment) smaller individuals encounter more substrates that support them during quadrupedalism (Fleagle and Mittermeier, 1980). This phenomenon has also been invoked to explain differences in frequencies of arboreal

quadrupedalism in general and arboreal knuckle-walking quadrupedalism specifically, both between *P. t. verus* and *P. t. schweinfurthii* and between the sexes within subspecies of *P. t. verus*, as larger arboreal substrates (relative to body size) are also more conducive to knuckle walking rather than palmigrade quadrupedalism (Doran and Hunt, 1994). This highlights the importance of considering the effects of the environment, such as substrate availability, on taxonomic patterns of locomotor behavior.

Lastly, it is worth noting that neither the phalanx nor the metacarpal or metatarsal are perfectly arc-shaped when viewed laterally, and that deviations from regular arc-shaped curvature may have functional implications that are obscured by this modeling technique. In recent years, alternative methods of modeling curvature have been developed that take these into account. Although results are generally in agreement with the more simple included angle measurements, they have on occasion resulted in different interpretations of the extent of arboreal behavior in some individuals (Deane and Begun, 2008; 2010). Similarly, the mediolateral variation in metacarpal/metatarsal dorsal ridge morphology mentioned above may be functionally informative, but is not captured by the current study. Developing alternate methods of quantifying these morphological variables may result in different interpretations of their links with behavior.

5.2 LIMITATIONS

Overall, interpretation of current study results in relation to hypothesized predictions was complicated by several factors. Most notably, small sample sizes for infants, especially *P. paniscus*, made it difficult to visualize and impossible to statistically test ontogenetic patterns prior to two years of age. This is unfortunate, as evidence from gorillas shows that this age range can incorporate relatively large changes in morphology

and is important for the evaluation of overall ontogenetic trends (Ruff et al., 2018). Without larger samples of bonobo and common chimpanzee infants in skeletal collections, this problem is difficult to surmount, but additional data from this age range are crucial to confirm the patterns discussed in the current study. The possibility of systematic errors in estimated ages related to subtle taxonomic differences in dental development should also be considered when interpreting results, especially given that there are some individuals in some taxa that are close to the boundaries of age categories (which themselves may be associated with some error).

An additional difficulty is presented by uncertainty in the degree and extent of geographic, environmental, and behavioral variation within *P. paniscus* or any single *P. troglodytes* subspecies, which have major implications for the interpretation of the relationship between morphology and behavior at that taxonomic level. For example, the morphological data used in this study span a much wider geographic area than the behavioral data have sampled: two of the taxa included have reasonably complete behavioral data available only from a single site, so comparing morphology and behavior assumes that this site is representative of the behavior of the taxon across its entire range, which may not be the case. Even when multiple sites are available (as for *P. t. schweinfurthii*, for which the Ngogo chimpanzees differ substantially from others), interpretation is complicated, as morphological results are sometimes more consistent with behavioral observations of one population than with another. All studies using observational data from wild primates are also potentially impacted by observer effects, as it is difficult to know the extent to which the presence of an observer is impacting the recorded behaviors (and this may be further compounded when including immature

individuals, which in theory might become increasingly habituated to observers' presence with age).

The above problems are likely to persist until better data on behavioral variation across more populations are available. It is worth noting that studies comparing some aspects of cross-sectional geometry with behavior within the individuals in a single population also do not return consistent results, although the mechanical interpretation of the particular characteristic studied (degree of section circularity) is not straightforward (Carlson et al., 2008; 2010).

5.3 Broader implications and Conclusions

This study found that differences in length and articular proportions between taxa in *Pan* tended to distinguish *P. paniscus* from all *P. troglodytes* subspecies, rather than *P. troglodytes* subspecies from each other, while cross-sectional geometry showed more differences between *P. troglodytes* subspecies, some of which were more similar to *P. paniscus* than others. Inter-limb cross-sectional strength proportions and phalangeal curvature generally tracked behavior both across adults and during ontogeny (with some exceptions), and dorsal metacarpal ridge morphology appeared to be related to both body size and to knuckle walking, although interpretation was complicated by the lack of detailed behavioral and postural data. This study also found differences in cross-sectional geometry within *P. troglodytes* subspecies, which should be taken into account in future studies comparing *P. troglodytes* with other taxa, especially in relatively fine-grained taxonomic analyses.

Overall, these results support the results of previous studies suggesting that bone length and strength proportions are under different amounts of genetic control and change at different rates on the evolutionary timescale: length ratios seem to be relatively canalized and perhaps reflect what an individual is capable of doing, while strengths appear to be more developmentally plastic and reflect the behaviors the individual performed during life. Phalangeal curvature was less strongly associated with behavior than expected, which could be for a variety of reasons, but suggests that a degree of caution is warranted in using this morphology to interpret arboreal behavior in fossils. The dorsal metacarpal ridge was clearly related to body size in all taxa, but the systematic differences between bonobos and *P. troglodytes* despite similarity in body size to *P. t. schweinfurthii* indicates additional factors at work, perhaps related to overall bone length proportions or to more subtle kinematic differences in knuckle walking.

The patterns discussed in this study are complex, and their interpretation is complicated by both a lack of adequate samples in some age ranges and a lack of detailed behavioral data. Collection of even basic locomotor and kinematic data on wild populations is challenging and time-consuming, but crucial to our understanding of the genus *Pan*. Further work is clearly needed to characterize basic behavioral patterns in chimpanzees at a variety of sites in order to more fully capture the degree and nature of behavioral variation in this taxon both within and among subspecies, including collection of behavioral data for *P. t. troglodytes.*

6 APPENDIX

Table 6.1 Adult locomotor frequencies by site

			Overall					Arboreal					
Taxon	**Population**	**Sex**	**Quad**	**C&S**	**Susp**	**Bipedal**	**Leap**	**Quad**	**C&S**	**Susp**	**Bipedal**	**Leap**	**% Arb****
P. t. schweinfurthii	Gombe	M	96.5	3.5	0	0	0	31.2	58.8	6.8	2.6	0.5	37.4
		F	89.5	8.9	0.5	1.1	0						68.4
	Mahale	M	93.6	5.1	0.8	0.3	0.2	25	65.6	7.8	1.6	0	32.9
		F	91.3	7.7	0.9	0.2	0	33.7	54.2	8.4	2.4	1.2	47.8
	Ngogo	M&F	77.5	14.5	6.19	1.8	0	--	--	--	--	--	--
P. t. verus	Taï Forest	M	86.6	11.1	1.1	1.2	0	11.7	76.7	5.8	5.8	0	48.9
		F	85.6	10.9	1.4	1.2	0.6	30.3	59.8	7.4	0.8	1.6	64.8
P. paniscus	Lui Kotale	M	97.9	1.9	0.1	0.2	0	16	74.9	2.9	6.3	0	41.3
		F	98.1	1.7	0	0.1	0	20.9	70.8	1.1	5.4	0	47.3
	Lomako†	M	--	--	--	--	--	26.1	57.9	19	1.1	4.8	--
		F	--	--	--	--	--	44.4	42.8	7.8	1.9	3.1	--

* See text for description of each category. Data for *P.t.schweinfurthii* (Gombe, Mahale), *P. t. verus*, and *P. paniscus* (Lomako) from Doran, 1996, tables 16.3 and 16.5; arboreal data for Mahale *P. t. schweinfurthii* from Doran & Hunt, 1994, table 6; data for *P. paniscus* (Lui Kotale) from Ramos, 2013; data for *P. t. schweinfurthii* (Ngogo) Sarringhaus et al., 2013.

** Percent of total observation time spent above the ground

† Impacted by incomplete habituation

Table 6.2 Ontogenetic locomotor frequencies by site

			Overall						Arboreal					
Taxon	**Population**	**Age**	**Quad**	**C&S**	**Susp**	**CS/Susp****	**Bipedal**	**Leap**	**Quad**	**C&S**	**Susp**	**CS/Susp****	**Bipedal**	**Leap**
P. t. s	Ngogo	Young inf	5.9	--	--	87.8	5.9	0.0	--	--	--	--	--	--
		Old inf	21.3	--	--	67.2	6.1	1.5	--	--	--	--	--	--
		Juv	47.6	30.9	18.8	49.7	2.2	0.0	--	--	--	--	--	--
		Adol	66.5	66.5	10.6	32.0	0.8	0.7	--	--	--	--	--	--
		Adult	77.5	14.5	6.2	20.7	1.8	0.0	--	--	--	--	--	--
P. t. v	Taï Forest	Young inf	10.7	52.9	27.9	80.8	7.3	0.7	14.92	54.84	27.50	82.35	2.47	0.61
		Old inf	66.2	23.1	8.6	31.7	1.0	1.0						
		Juv	92.5	6.3	0.9	7.2	0.2	0.0	22.5	67	9.2	76.2	0.9	0
		Adol	95.1	95.1	0.1	5.5	0.2	0.1	24.1	71.7	2.2	73.9	1.1	0.9
		Adult	86.1	11.0	1.2	12.2	1.2	0.3	21.8	71	5.3	76.3	0.7	1.1
P. p	Lomako†	Infant	--	--	--	--	--	--	31.7	43.7	19.1	62.8	1.1	4.4
		Juv	--	--	--	--	--	--	36.8	44	13	57	0.5	5.6
		Adol	--	--	--	--	--	--	38.2	47.4	9.9	57.3	0.7	3.8
		Ad	--	--	--	--	--	--	35.7	48.9	10.3	59.2	1.3	3.8

* Data for P. t. schweinfurthii from Sarringhaus et al., 2015; Data for P. t. verus and P.paniscus from Doran 1989 (Table 6.13, 6.15), 1992

** Derived from calculated raw counts of combined climbing and scrambling and suspensory behavior (see text)

† Impacted by incomplete habituation

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Table 6.3 Summary statistics for lengths and length ratios within subspecies/age groups

	Young infant							
	P. pan.		***P. t. schw.***		***P. t. trog.***		***P. t. ver.***	
	n	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**
FLd	1	102.00 (NA)	2	70.21 (20.92)	6	104.36 (8.10)	6	91.67 (21.93)
TLd	1	105.00 (NA)	2	72.46 (21.98)	6	108.50 (8.64)	6	95.30 (21.90)
HLd	1	86.00 (NA)	2	62.10 (19.66)	6	90.80 (6.63)	6	78.68 (17.23)
RLd	1	102.00 (NA)	2	68.74 (18.76)	6	103.62 (8.11)	6	89.99 (20.90)
ULd	1	105.00 (NA)	2	70.53 (17.64)	6	112.52 (8.97)	5	95.06 (25.24)
MCLd	1	34.28 (NA)	2	22.66 (7.58)	6	34.02 (1.80)	5	30.95 (6.18)
MTLd	1	25.64 (NA)	1	22.44 (NA)	6	25.54 (1.90)	5	25.65 (3.29)
PLd	1	24.65 (NA)	2	18.30 (5.46)	6	26.69 (1.25)	5	23.94 (4.53)
FHLd	1	-0.029 (NA)	2	-0.031 (0.006)	6	-0.039 (0.019)	6	-0.041 (0.013)
FLHLd	1	5.322 (NA)	2	4.920 (0.288)	6	5.339 (0.078)	6	5.183 (0.243)
TRLd	1	-0.171 (NA)	2	-0.108 (0.046)	6	-0.132 (0.015)	6	-0.132 (0.018)
TFLd	1	-0.171 (NA)	2	-0.126 (0.020)	6	-0.139 (0.015)	6	-0.149 (0.026)
RHLd	1	-0.029 (NA)	2	-0.048 (0.032)	6	-0.046 (0.019)	6	-0.058 (0.018)
URLd	1	0.029 (NA)	2	0.029 (0.024)	6	0.082 (0.019)	5	0.071 (0.011)
MTMCLd	1	-0.290 (NA)	1	-0.222 (NA)	6	-0.288 (0.031)	4	-0.236 (0.019)
MCHLd	1	-1.119 (NA)	2	-1.168 (0.033)	6	-1.158 (0.071)	5	-1.121 (0.068)
MTFLd	1	-1.381 (NA)	1	-1.332 (NA)	6	-1.407 (0.050)	5	-1.325 (0.076)
MCPLd	1	-0.330 (NA)	2	-0.208 (0.038)	6	-0.243 (0.023)	5	-0.255 (0.025)

	Old infant							
	P. pan.		***P. t. schw.***		***P. t. trog.***		***P. t. ver.***	
	n	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**
FLd	5	132.37 (8.02)	7	136.03 (15.88)	9	138.78 (14.42)	2	143.97 (26.91)
TLd	6	138.87 (8.49)	7	144.16 (17.63)	9	147.44 (13.84)	2	152.50 (24.75)
HLd	6	113.37 (7.24)	7	114.71 (13.07)	9	117.93 (10.31)	2	118.50 (20.51)
RLd	6	132.11 (9.02)	7	132.19 (14.27)	9	138.22 (11.37)	2	139.00 (25.46)
ULd	6	139.91 (9.32)	7	142.57 (16.93)	9	148.89 (12.24)	2	149.50 (26.16)
MCLd	5	39.20 (0.80)	6	41.15 (4.13)	9	43.16 (3.84)	1	37.64 (NA)
MTLd	5	29.72 (2.05)	5	30.68 (3.08)	9	32.59 (2.96)	1	29.45 (NA)
PLd	3	29.46 (2.95)	5	29.56 (2.95)	9	33.12 (2.82)	0	NA (NA)
FHLd	5	-0.043 (0.011)	7	-0.057 (0.022)	9	-0.061 (0.030)	2	-0.060 (0.025)
FLHLd	5	5.578 (0.067)	7	5.589 (0.114)	9	5.623 (0.091)	2	5.639 (0.186)
TRLd	6	-0.153 (0.029)	7	-0.142 (0.017)	9	-0.159 (0.015)	2	-0.159 (0.010)
TFLd	5	-0.158 (0.016)	7	-0.170 (0.034)	9	-0.161 (0.025)	2	-0.193 (0.014)
RHLd	6	-0.050 (0.031)	7	-0.085 (0.026)	9	-0.064 (0.036)	2	-0.095 (0.021)
URLd	6	0.058 (0.011)	7	0.075 (0.016)	9	0.074 (0.010)	2	0.074 (0.008)
MTMCLd	5	-0.279 (0.053)	5	-0.272 (0.036)	9	-0.281 (0.032)	1	-0.245 (NA)
MCHLd	5	-1.252 (0.048)	6	-1.231 (0.048)	9	-1.228 (0.068)	1	-1.277 (NA)
MTFLd	4	-1.494 (0.019)	5	-1.442 (0.080)	9	-1.448 (0.079)	1	-1.445 (NA)
MCPLd	3	-0.286 (0.103)	5	-0.334 (0.031)	9	-0.264 (0.042)	0	NA (NA)

Table 6.3, cont'd

Juv

	P. pan.		P. t. schw.		P. t. trog.		P. t. ver.	
	n	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**
FLd	8	186.99 (23.07)	12	197.40 (21.92)	22	186.55 (17.18)	7	190.55 (17.39)
TLd	8	189.41 (22.97)	12	202.33 (21.25)	22	195.18 (16.37)	9	198.29 (13.78)
HLd	8	153.17 (19.36)	12	163.82 (18.85)	22	156.32 (14.53)	5	152.40 (12.42)
RLd	8	173.29 (19.51)	12	185.22 (20.77)	22	182.45 (15.58)	9	178.33 (13.30)
ULd	8	184.73 (20.16)	12	201.80 (23.61)	22	197.36 (17.48)	8	195.00 (14.76)
MCLd	6	53.80 (6.02)	9	58.76 (7.91)	22	54.62 (6.00)	8	54.53 (5.38)
MTLd	6	40.54 (5.83)	9	45.35 (5.58)	21	41.81 (4.67)	5	42.29 (4.25)
PLd	4	36.60 (5.14)	2	43.62 (2.96)	22	41.28 (4.21)	7	39.82 (3.12)
FHLd	8	-0.013 (0.021)	12	-0.026 (0.024)	22	-0.046 (0.031)	7	-0.052 (0.023)
FLHLd	8	5.884 (0.110)	12	5.943 (0.113)	22	5.909 (0.088)	5	5.909 (0.087)
TRLd	8	-0.125 (0.025)	12	-0.123 (0.029)	22	-0.155 (0.026)	5	-0.164 (0.021)
TFLd	8	-0.200 (0.014)	12	-0.187 (0.036)	22	-0.177 (0.026)	5	-0.215 (0.042)
RHLd	8	-0.088 (0.030)	12	-0.089 (0.030)	22	-0.068 (0.031)	9	-0.106 (0.017)
URLd	8	0.064 (0.010)	12	0.085 (0.013)	22	0.078 (0.013)	8	0.078 (0.007)
MTMCLd	6	-0.286 (0.030)	9	-0.257 (0.021)	21	-0.276 (0.043)	5	-0.273 (0.022)
MCHLd	6	-1.265 (0.039)	9	-1.234 (0.039)	22	-1.276 (0.060)	8	-1.283 (0.056)
MTFLd	6	-1.530 (0.042)	9	-1.462 (0.041)	21	-1.502 (0.055)	5	-1.499 (0.065)
MCPLd	4	-0.410 (0.018)	2	-0.340 (0.042)	22	-0.279 (0.051)	7	-0.325 (0.037)

Adol

	P. pan.		P. t. schw.		P. t. trog.		P. t. ver.	
	n	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**
FLd	8	250.95 (17.04)	7	255.78 (13.71)	6	262.66 (15.51)	7	251.30 (18.00)
TLd	8	250.04 (16.95)	7	259.77 (14.44)	6	268.51 (13.25)	7	256.60 (17.93)
HLd	7	208.63 (13.99)	7	211.72 (11.03)	6	216.06 (10.75)	5	207.91 (12.75)
RLd	8	230.34 (14.39)	7	235.92 (13.44)	6	243.16 (13.52)	6	231.58 (19.27)
ULd	8	246.79 (16.68)	7	257.18 (15.18)	6	265.47 (16.05)	6	257.74 (14.88)
MCLd	8	71.63 (5.46)	7	72.99 (4.69)	6	70.62 (4.06)	6	69.70 (6.15)
MTLd	8	55.64 (3.92)	7	58.27 (4.60)	5	57.01 (3.39)	6	54.50 (4.95)
PLd	7	49.97 (5.48)	2	53.41 (5.88)	6	52.27 (4.76)	4	50.57 (3.26)
FHLd	8	0.004 (0.016)	7	-0.015 (0.019)	6	-0.022 (0.022)	7	-0.021 (0.012)
FLHLd	7	6.181 (0.066)	7	6.198 (0.050)	6	6.227 (0.050)	5	6.197 (0.062)
TRLd	7	-0.103 (0.016)	7	-0.108 (0.020)	6	-0.118 (0.041)	5	-0.130 (0.024)
TFLd	7	-0.191 (0.028)	7	-0.189 (0.029)	6	-0.195 (0.041)	5	-0.202 (0.009)
RHLd	8	-0.082 (0.017)	7	-0.096 (0.039)	6	-0.099 (0.043)	6	-0.095 (0.020)
URLd	8	0.069 (0.008)	7	0.086 (0.007)	6	0.088 (0.007)	5	0.079 (0.006)
MTMCLd	8	-0.252 (0.021)	7	-0.226 (0.030)	5	-0.224 (0.028)	6	-0.246 (0.026)
MCHLd	8	-1.251 (0.041)	7	-1.270 (0.058)	6	-1.336 (0.042)	6	-1.296 (0.049)
MTFLd	8	-1.507 (0.044)	7	-1.481 (0.078)	5	-1.539 (0.054)	6	-1.521 (0.056)
MCPLd	7	-0.366 (0.069)	2	-0.349 (0.018)	6	-0.303 (0.056)	4	-0.350 (0.054)

Table 6.4 Summary statistics for cross-sectional variables within subspecies/age groups

	Young inf							
	P. pan.		***P. t. schw.***		***P. t. trog.***		***P. t. ver.***	
	n	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**
FHZp	1	-0.066(NA)	1	-0.007(NA)	6	-0.025(0.11)	6	-0.151(0.19)
TRZp	1	0.480(NA)	1	0.341(NA)	6	0.289(0.24)	6	0.127(0.17)
TFZp	1	-0.579(NA)	1	-0.759(NA)	6	-0.716(0.08)	6	-0.783(0.11)
RHZp	1	-1.124(NA)	1	-1.107(NA)	6	-1.029(0.22)	6	-1.060(0.13)
URZp	1	-0.203(NA)	1	-0.264(NA)	6	-0.227(0.19)	5	-0.444(0.11)
MTMCZp	1	-0.960(NA)	1	-0.731(NA)	6	-0.593(0.12)	4	-0.592(0.16)
MCHZp	1	-1.840(NA)	1	-2.214(NA)	6	-2.166(0.07)	5	-2.426(0.14)
MTRZp	1	-2.735(NA)	1	-2.938(NA)	6	-2.734(0.12)	5	-2.901(0.13)
FZp/(BM*BL)	1	-1.659(NA)	1	-1.238(NA)	6	-1.472(0.13)	6	-1.161(0.34)
HZp/(BM*BL)	1	-1.622(NA)	1	-1.266(NA)	6	-1.486(0.21)	6	-1.051(0.36)
TZp/(BM*BL)	1	-2.067(NA)	1	-1.885(NA)	6	-2.049(0.13)	6	-1.795(0.28)
RZp/(BM*BL)	1	-2.717(NA)	1	-2.302(NA)	6	-2.469(0.25)	6	-2.054(0.36)
UZp/(BM*BL)	1	-2.949(NA)	1	-2.578(NA)	6	-2.779(0.26)	5	-2.594(0.39)
MCZp/(BM*BL)	1	-2.343(NA)	1	-2.335(NA)	6	-2.493(0.19)	5	-2.406(0.38)
MTZp/(BM*BL)	1	-3.013(NA)	1	-2.844(NA)	6	-2.799(0.17)	5	-2.818(0.24)
FZxZy	1	1.144(NA)	1	1.064(NA)	6	0.997(0.06)	6	0.992(0.04)
HZxZy	1	1.112(NA)	1	0.862(NA)	6	0.964(0.04)	6	1.053(0.04)
TZxZy	1	1.175(NA)	1	1.018(NA)	6	1.097(0.10)	6	1.117(0.08)
RZxZy	1	0.978(NA)	1	0.843(NA)	6	0.962(0.03)	6	0.999(0.10)
UZxZy	1	0.886(NA)	1	1.103(NA)	6	1.064(0.07)	5	1.090(0.09)
MCZxZy	1	1.114(NA)	1	0.968(NA)	6	1.050(0.10)	5	1.032(0.07)
MTZxZy	1	1.438(NA)	1	1.321(NA)	6	1.288(0.08)	5	1.243(0.07)

Table 6.4, cont'd

	Old inf							
	P. pan.		***P. t. schw.***		***P. t. trog.***		***P. t. ver.***	
	n	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**
FHZp	5	0.209(0.10)	7	0.105(0.07)	9	0.116(0.07)	2	-0.057(0.04)
TRZp	6	0.727(0.14)	7	0.468(0.22)	9	0.436(0.12)	2	0.362(0.07)
TFZp	5	-0.598(0.24)	7	-0.784(0.11)	9	-0.702(0.14)	2	-0.698(0.12)
RHZp	6	-1.099(0.12)	7	-1.147(0.14)	9	-1.022(0.26)	2	-1.117(0.08)
URZp	5	0.051(0.15)	7	-0.148(0.15)	9	-0.201(0.19)	2	-0.300(0.10)
MTMCZp	4	-0.571(0.04)	5	-0.515(0.23)	9	-0.532(0.16)	1	-0.618(NA)
MCHZp	4	-2.057(0.10)	5	-2.364(0.18)	9	-2.228(0.16)	1	-2.557(NA)
MTRZp	3	-2.913(0.17)	5	-2.961(0.32)	9	-2.876(0.24)	1	-3.090(NA)
FZp/(BM*BL)	5	-1.687(0.26)	7	-1.731(0.18)	9	-1.609(0.20)	2	-1.475(0.13)
HZp/(BM*BL)	6	-1.909(0.28)	7	-1.893(0.20)	9	-1.786(0.26)	2	-1.477(0.14)
TZp/(BM*BL)	6	-2.079(0.29)	7	-2.344(0.18)	9	-2.149(0.23)	2	-1.979(0.01)
RZp/(BM*BL)	6	-2.958(0.25)	7	-2.955(0.30)	9	-2.744(0.31)	2	-2.500(0.08)
UZp/(BM*BL)	5	-3.003(0.34)	7	-3.178(0.22)	9	-3.019(0.27)	2	-2.873(0.18)
MCZp/(BM*BL)	4	-2.815(0.29)	5	-2.960(0.32)	9	-2.786(0.26)	1	-2.657(NA)
MTZp/(BM*BL)	4	-3.102(0.31)	5	-3.203(0.32)	9	-3.037(0.25)	1	-3.030(NA)
FZxZy	5	1.079(0.05)	7	0.966(0.02)	9	0.991(0.07)	2	0.939(0.02)
HZxZy	6	1.115(0.07)	7	1.017(0.06)	9	1.063(0.08)	2	1.107(0.03)
TZxZy	6	1.271(0.04)	7	1.260(0.11)	9	1.176(0.08)	2	1.162(0.04)
RZxZy	6	1.042(0.10)	7	0.923(0.06)	9	1.009(0.09)	2	1.014(0.01)
UZxZy	5	1.162(0.10)	7	1.002(0.07)	9	1.023(0.08)	2	1.044(0.02)
MCZxZy	4	1.041(0.09)	5	1.054(0.12)	9	1.013(0.06)	1	1.182(NA)
MTZxZy	4	1.254(0.11)	5	1.298(0.12)	9	1.247(0.12)	1	1.361(NA)

Table 6.4, cont'd

	Juv							
	P. pan.		***P. t. schw.***		***P. t. trog.***		***P. t. ver.***	
	n	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**
FHZp	8	0.359(0.13)	12	0.229(0.12)	22	0.187(0.10)	7	0.131(0.07)
TRZp	8	0.841(0.05)	12	0.702(0.15)	22	0.736(0.14)	5	0.592(0.18)
TFZp	8	-0.667(0.10)	12	-0.724(0.13)	22	-0.619(0.23)	5	-0.634(0.17)
RHZp	8	-1.149(0.06)	12	-1.197(0.13)	22	-1.168(0.27)	9	-1.106(0.09)
URZp	8	0.076(0.12)	12	0.083(0.16)	20	-0.035(0.13)	9	-0.211(0.11)
MTMCZp	6	-0.401(0.16)	8	-0.465(0.16)	21	-0.432(0.09)	5	-0.460(0.09)
MCHZp	6	-2.241(0.19)	9	-2.340(0.07)	22	-2.366(0.18)	8	-2.454(0.12)
MTRZp	6	-3.041(0.23)	8	-3.021(0.19)	21	-2.985(0.21)	5	-3.036(0.08)
FZp/(BM*BL)	8	-1.828(0.25)	12	-1.661(0.16)	22	-1.557(0.18)	7	-1.489(0.18)
HZp/(BM*BL)	8	-2.200(0.28)	12	-1.916(0.25)	22	-1.790(0.20)	9	-1.703(0.17)
TZp/(BM*BL)	8	-2.295(0.31)	12	-2.198(0.23)	22	-1.999(0.28)	5	-1.883(0.16)
RZp/(BM*BL)	8	-3.261(0.31)	12	-3.024(0.32)	22	-2.890(0.31)	9	-2.704(0.14)
UZp/(BM*BL)	8	-3.248(0.36)	12	-3.027(0.27)	20	-2.990(0.28)	8	-2.999(0.14)
MCZp/(BM*BL)	6	-3.198(0.37)	9	-3.013(0.21)	22	-2.880(0.19)	8	-2.911(0.19)
MTZp/(BM*BL)	6	-3.313(0.31)	8	-3.244(0.31)	21	-3.042(0.21)	5	-3.001(0.14)
FZxZy	8	0.988(0.07)	12	0.965(0.06)	22	0.952(0.06)	7	0.870(0.05)
HZxZy	8	1.100(0.07)	12	0.999(0.05)	22	1.041(0.05)	10	1.100(0.05)
TZxZy	8	1.384(0.08)	12	1.413(0.12)	22	1.363(0.12)	5	1.280(0.05)
RZxZy	8	0.985(0.10)	12	0.948(0.07)	22	0.941(0.07)	9	1.017(0.08)
UZxZy	8	1.004(0.11)	12	1.094(0.12)	20	1.061(0.12)	9	1.064(0.08)
MCZxZy	6	1.104(0.09)	9	0.976(0.10)	22	0.970(0.07)	8	0.947(0.09)
MTZxZy	6	1.332(0.06)	8	1.293(0.16)	21	1.342(0.11)	5	1.277(0.08)

Table 6.4, cont'd

	Adol							
	P. pan.		***P. t. schw.***		***P. t. trog.***		***P. t. ver.***	
	n	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**
FHZp	8	0.375(0.08)	7	0.281(0.08)	6	0.201(0.06)	7	0.163(0.11)
TRZp	7	0.886(0.11)	7	0.848(0.17)	6	0.817(0.12)	5	0.743(0.13)
TFZp	7	-0.640(0.07)	7	-0.710(0.06)	6	-0.587(0.22)	5	-0.619(0.08)
RHZp	8	-1.148(0.09)	7	-1.278(0.13)	6	-1.204(0.24)	6	-1.215(0.12)
URZp	8	-0.075(0.11)	7	0.003(0.17)	6	0.007(0.13)	4	-0.108(0.18)
MTMCZp	8	-0.454(0.06)	7	-0.433(0.15)	5	-0.398(0.13)	6	-0.550(0.29)
MCHZp	8	-2.284(0.05)	7	-2.408(0.11)	6	-2.425(0.20)	6	-2.469(0.14)
MTRZp	8	-3.113(0.05)	7	-3.123(0.10)	5	-2.999(0.19)	6	-3.184(0.27)
FZp/(BM*BL)	8	-2.109(0.14)	6	-1.852(0.14)	6	-1.432(0.34)	6	-1.534(0.31)
HZp/(BM*BL)	8	-2.481(0.14)	6	-2.163(0.15)	6	-1.656(0.31)	6	-1.720(0.31)
TZp/(BM*BL)	7	-2.568(0.15)	6	-2.375(0.18)	6	-1.825(0.33)	5	-1.972(0.32)
RZp/(BM*BL)	8	-3.548(0.20)	6	-3.339(0.11)	6	-2.760(0.45)	6	-2.840(0.26)
UZp/(BM*BL)	8	-3.691(0.22)	6	-3.418(0.16)	6	-2.841(0.34)	4	-3.020(0.27)
MCZp/(BM*BL)	8	-3.514(0.17)	6	-3.301(0.19)	6	-2.745(0.29)	6	-2.893(0.35)
MTZp/(BM*BL)	8	-3.716(0.14)	6	-3.509(0.21)	5	-2.973(0.27)	6	-3.197(0.41)
FZxZy	8	0.939(0.09)	7	0.944(0.07)	6	0.925(0.09)	7	0.874(0.04)
HZxZy	8	1.081(0.06)	7	1.040(0.08)	6	1.023(0.07)	7	1.048(0.05)
TZxZy	7	1.426(0.06)	7	1.555(0.12)	6	1.524(0.11)	5	1.406(0.07)
RZxZy	8	0.921(0.06)	7	1.013(0.09)	6	0.986(0.08)	6	1.066(0.07)
UZxZy	8	1.006(0.07)	7	1.032(0.08)	6	1.048(0.12)	5	0.984(0.08)
MCZxZy	8	1.034(0.07)	7	0.988(0.06)	6	0.977(0.09)	6	0.964(0.05)
MTZxZy	8	1.443(0.10)	7	1.353(0.12)	5	1.319(0.11)	6	1.283(0.09)

Table 6.5 Summary statistics for joint/metaphyseal variables within subspecies/age groups (all metaphyseal values except for adolescents)

Young inf

	P. pan.		***P. t. schw.***		***P. t. trog.***		***P. t. ver.***	
	n	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**
FDML	1	24.36(NA)	2	18.82(7.45)	6	24.95(2.07)	6	23.61(4.13)
TPML	1	18.77(NA)	2	14.86(7.10)	6	20.32(1.91)	6	18.04(3.20)
HDML	1	25.36(NA)	2	19.35(7.53)	6	26.18(1.79)	6	25.77(3.99)
RHML	1	8.72(NA)	2	7.89(2.70)	6	8.98(0.72)	6	9.62(1.39)
UPML	1	7.98(NA)	2	5.98(0.77)	6	8.01(0.61)	6	8.00(2.12)
FD/HD	1	-0.040(NA)	2	-0.029(0.007)	6	-0.049(0.061)	6	-0.090(0.044)
TP/RH	1	0.767(NA)	2	0.603(0.148)	6	0.816(0.050)	6	0.625(0.065)
TP/FD	1	-0.261(NA)	2	-0.256(0.091)	6	-0.206(0.035)	6	-0.270(0.040)
RH/HD	1	-1.068(NA)	2	-0.888(0.050)	6	-1.071(0.021)	6	-0.985(0.037)
UP/HD	1	-1.156(NA)	2	-1.140(0.270)	6	-1.185(0.072)	6	-1.186(0.146)
UP/RH	1	-0.089(NA)	2	-0.252(0.220)	6	-0.114(0.072)	6	-0.201(0.169)

Old Inf

	P. pan.		***P. t. schw.***		***P. t. trog.***		***P. t. ver.***	
	n	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**
FDML	4	29.11(2.02)	7	32.87(4.65)	8	32.35(3.01)	2	32.05(3.32)
TPML	4	23.47(1.28)	6	25.58(4.05)	8	26.17(2.83)	2	27.32(5.09)
HDML	4	28.48(0.18)	7	32.27(3.22)	9	31.46(2.50)	2	35.22(4.86)
RHML	3	10.34(0.27)	7	11.91(0.84)	8	11.28(1.03)	2	12.14(1.67)
UPML	4	10.05(0.20)	7	10.99(1.15)	8	10.60(1.63)	2	12.66(2.26)
FD/HD	2	0.026(0.029)	7	0.014(0.078)	8	0.018(0.032)	2	-0.092(0.035)
TP/RH	3	0.800(0.029)	6	0.765(0.151)	8	0.840(0.073)	2	0.807(0.050)
TP/FD	2	-0.225(0.058)	6	-0.232(0.045)	8	-0.213(0.031)	2	-0.166(0.084)
RH/HD	3	-1.013(0.022)	7	-0.994(0.086)	8	-1.035(0.038)	2	-1.065(0.000)
UP/HD	4	-1.042(0.025)	7	-1.078(0.053)	8	-1.104(0.111)	2	-1.027(0.041)
UP/RH	3	-0.025(0.047)	7	-0.084(0.101)	8	-0.070(0.113)	2	0.038(0.041)

Table 6.5, cont'd

Juv

	P. pan.		*P. t. schw.*		*P. t. trog.*		*P. t. ver.*	
	n	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**
FDML	5	39.55(3.03)	5	40.81(2.29)	22	41.17(3.56)	6	40.10(4.45)
TPML	6	32.25(3.32)	5	34.18(2.01)	21	34.72(3.18)	4	34.03(3.94)
HDML	6	36.93(2.42)	5	40.73(3.25)	22	41.80(4.97)	9	44.53(5.71)
RHML	6	13.04(0.97)	4	14.53(1.62)	22	14.63(1.57)	9	15.65(1.94)
UPML	8	14.01(2.38)	11	15.90(2.32)	21	14.96(2.30)	9	15.95(2.08)
FD/HD	4	0.080(0.093)	4	0.002(0.109)	22	-0.012(0.058)	6	-0.125(0.074)
TP/RH	5	0.907(0.038)	2	0.915(0.025)	21	0.855(0.062)	4	0.790(0.098)
TP/FD	5	-0.200(0.058)	5	-0.177(0.051)	21	-0.181(0.052)	4	-0.134(0.063)
RH/HD	6	-1.041(0.081)	3	-1.025(0.045)	22	-1.049(0.062)	9	-1.045(0.080)
UP/HD	6	-1.035(0.132)	4	-1.080(0.038)	21	-1.025(0.079)	9	-1.027(0.042)
UP/RH	6	0.006(0.103)	4	0.006(0.121)	21	0.023(0.097)	9	0.018(0.106)

Adol

	P. pan.		*P. t. schw.*		*P. t. trog.*		*P. t. ver.*	
	n	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**
FDML	8	46.40(3.59)	7	49.38(5.72)	6	51.50(3.33)	5	48.95(4.76)
TPML	8	37.41(3.00)	7	40.48(3.62)	6	41.81(2.49)	6	40.38(3.11)
HDML	7	51.23(2.74)	6	53.43(3.87)	6	52.90(1.94)	4	52.49(4.86)
RHML	8	20.59(1.19)	5	22.04(1.78)	5	23.23(1.17)	6	23.14(2.66)
UPML	8	20.61(2.36)	6	22.17(0.86)	6	22.88(2.55)	6	22.59(2.78)
FD/HD	8	0.216(0.043)	7	0.196(0.074)	6	0.208(0.060)	5	0.201(0.046)
TP/RH	7	0.908(0.037)	4	0.868(0.048)	5	0.827(0.021)	4	0.846(0.036)
TP/FD	7	0.096(0.039)	6	0.070(0.062)	6	0.028(0.037)	4	0.066(0.020)
RH/HD	8	-0.596(0.052)	5	-0.602(0.079)	5	-0.595(0.061)	6	-0.560(0.054)
UP/HD	8	-0.599(0.069)	6	-0.616(0.068)	6	-0.607(0.085)	6	-0.584(0.067)
UP/RH	8	-0.003(0.099)	4	-0.010(0.042)	5	-0.015(0.105)	6	-0.025(0.077)

Table 6.6 Summary statistics for curvature within subspecies/age groups

Young inf

	P. pan.		*P. t. schw.*		*P. t. trog.*		*P. t. ver.*	
	n	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**
MCIA	1	32.33(NA)	2	30.97(2)	6	26.57(2)	4	27.02(3)
MTIA	1	34.48(NA)	1	38.91(NA)	6	37.17(3)	5	32.95(6)
PIA	1	55.71(NA)	2	56.52(12)	6	62.77(4)	4	61.38(7)
MCNCMA	1	4.65(NA)	1	5.66(NA)	6	4.44(1)	4	4.60(1)
MTNCMA	1	10.66(NA)	1	12.53(NA)	6	9.81(1)	5	9.59(4)
PNCMA	1	8.01(NA)	1	12.53(NA)	6	10.58(2)	4	10.53(3)

Old inf

	P. pan.		*P. t. schw.*		*P. t. trog.*		*P. t. ver.*	
	n	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**
MCIA	3	27.74(5.32)	4	30.19(3.97)	9	27.82(3.78)	1	23.94(NA)
MTIA	2	35.01(4.76)	3	33.22(4.48)	9	37.30(6.05)	1	30.73(NA)
PIA	2	61.83(2.75)	3	54.64(4.74)	9	61.85(7.09)	0	NA(NA)
MCNCMA	3	3.65(0.15)	4	3.34(0.39)	9	2.80(0.87)	1	2.46(NA)
MTNCMA	2	6.13(0.09)	3	5.72(1.59)	9	5.52(2.31)	1	5.45(NA)
PNCMA	2	7.84(0.91)	3	6.60(0.90)	9	6.40(2.79)	0	NA(NA)

Juv

	P. pan.		*P. t. schw.*		*P. t. trog.*		*P. t. ver.*	
	n	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**
MCIA	6	31.71(4.48)	9	32.78(4.83)	22	32.47(4.04)	8	30.98(3.42)
MTIA	6	39.67(6.29)	7	37.39(2.67)	21	41.02(5.37)	5	41.52(5.30)
PIA	4	61.17(5.41)	2	52.62(4.19)	22	57.35(6.93)	7	52.90(10.35)
MCNCMA	6	1.74(0.42)	9	1.27(0.42)	22	1.54(0.55)	8	1.59(0.44)
MTNCMA	6	2.69(0.78)	7	1.98(0.59)	21	2.37(0.80)	5	2.71(0.78)
PNCMA	4	3.29(1.13)	2	1.64(0.36)	22	2.73(1.03)	7	2.61(0.60)

Adol

	P. pan.		*P. t. schw.*		*P. t. trog.*		*P. t. ver.*	
	n	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**	**n**	**mean(SD)**
MCIA	8	37.23(3.22)	6	36.78(4.26)	6	32.85(4.32)	6	37.40(2.09)
MTIA	8	42.78(3.54)	6	44.20(4.83)	5	39.05(4.83)	6	47.58(12.40)
PIA	7	59.22(5.22)	3	62.44(4.95)	6	60.59(6.67)	3	53.76(5.08)
MCNCMA	8	0.93(0.20)	6	0.71(0.12)	6	0.59(0.15)	6	0.80(0.29)
MTNCMA	8	1.33(0.28)	6	1.06(0.17)	5	0.78(0.15)	6	1.50(0.65)
PNCMA	7	1.48(0.43)	3	1.29(0.18)	6	1.08(0.18)	3	1.05(0.42)

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8 CURRICULUM VITAE

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Education

2011–2018	Ph.D., Functional Anatomy and Evolution The Johns Hopkins University School of Medicine Dissertation: "*Ontogenetic Change in Limb Bone Structural Properties and Behavior in* Pan" Advisor: Dr. Christopher B. Ruff
2011	B.A., Anthropology New York University Magna cum Laude with Honors

Honors and Awards

2011	Phi Beta Kappa, New York University
2008 – 2011	Member, Presidential Honors Scholars Society (New York University)

Academic and Research Appointments

2016	Student Research Associate, Smithsonian institute of Natural History, Washington DC

Grants

2015, 2016	William S. Pollitzer Student Travel Award (American Association of Physical Anthropologists)
2012	Graduate Student Travel Award (Johns Hopkins School of Medicine)
2010	Dean's Undergraduate Research Fund Grant (New York University)

Publications

PAPERS

Ruff, C.B., **Burgess, M.L.,** Junno, J.-A., Mudakikwa, A., Zollikofer, C.P.E., Ponce de León, M.S., McFarlin, S.C. (2018). Phylogenetic and environmental effects on limb bone structure in gorillas. Am. J. Phys. Anthropol. *(Epub ahead of print, DOI: 10.1002/ajpa.23437)*

Burgess, M.L., Schmitt, D., Zeininger, A., McFarlin, S.C., Zihlman, A.L., Polk, J.D., Ruff, C.B. (2016). Ontogenetic scaling of fore- and hindlimb joint posture and limb bone cross-sectional geometry in vervets and baboons. Am. J. Phys. Anthropol. 161:72-83.

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Teaching experience

2014, 2015 Gross Anatomy for PA Students (Towson University/CCBC Essex)
Lecturer and lab instructor for gross anatomy course taught to first-year physician assistant students

2013-2015 Medical Anatomy Tutor (Johns Hopkins School of Medicine)
Tutored students in medical gross anatomy course and served as substitute lab instructor

2013-2014 Primate Adaptation and Evolution (Johns Hopkins University)
TA and additional lecturer for undergraduate introductory primate and human evolution course

2013 Medical Gross Anatomy (Johns Hopkins School of Medicine)
Lab instructor for medical gross anatomy course taught to first-year medical students and graduate students

2012, 2013 Summer Institute in Anatomy (Johns Hopkins School of Medicine)
Performed prosections and taught small lab sections for introductory undergraduate anatomy course

2012 Comparative Mammalian Anatomy (Student-run course)
Performed and filmed lectures on comparative dissections on vertebrates

2012-2015 Summer Anatomy Tutor (Johns Hopkins School of Medicine)
Tutored students in introductory undergraduate anatomy course

Professional Service

Program Representative to the Johns Hopkins University School of Medicine Graduate Student Association (2013—2014)
Co-founder, AAPA LGBTQ Resource Group
Social Media Outreach Coordinator, Johns Hopkins Summer Institute in Anatomy